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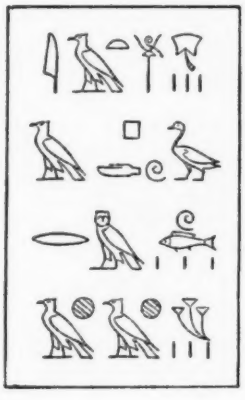

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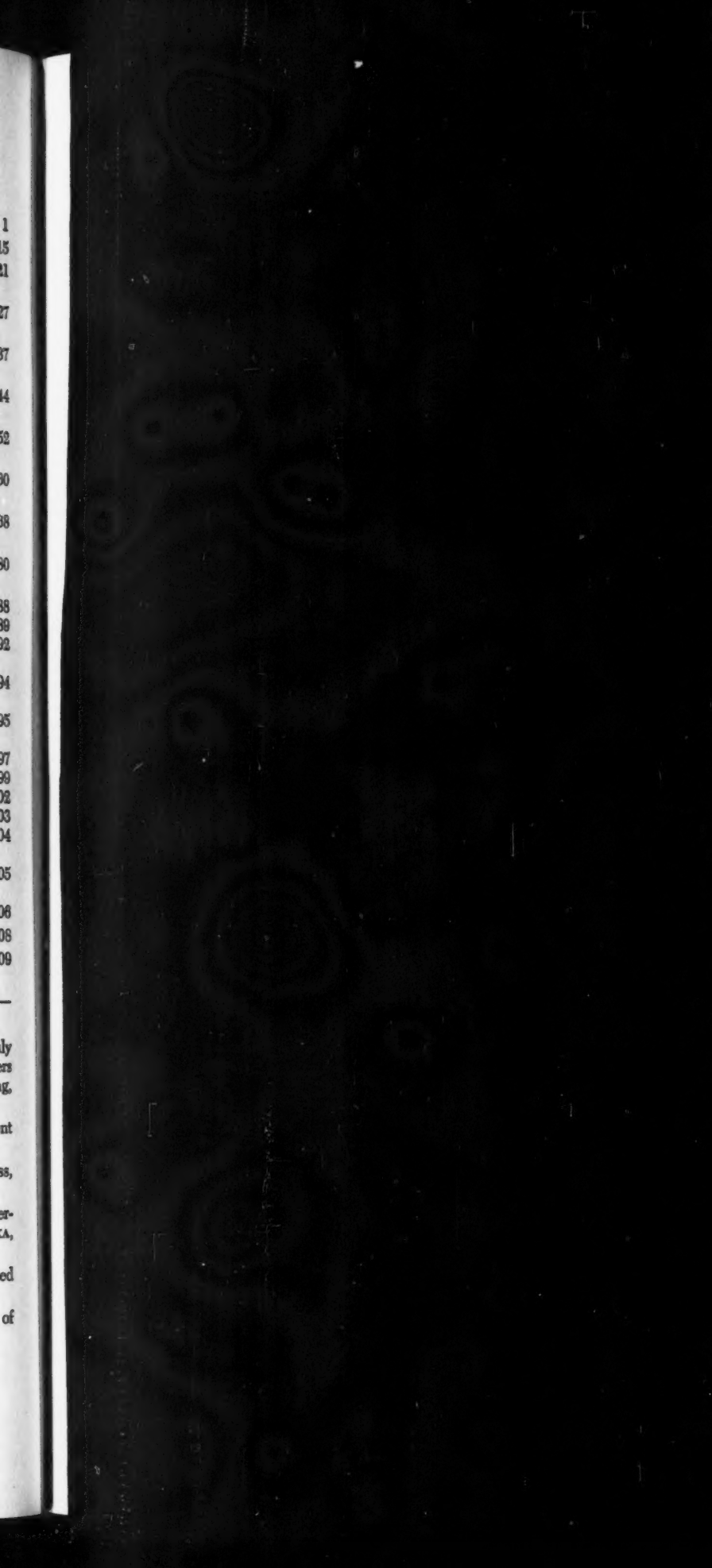

THE JOURNAL OF WILDLIFE MANAGEMENT

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PREDATION ON BIG GAME IN EAST AFRICA[1]

Bruce S. Wright

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A study of the food habits, hunting methods, and habitat requirements of the large predators was carried out in southern Kenya and central Tanganyika in 1957. Predation on large land mammals under primitive conditions in East Africa may be the heaviest in the world. This paper describes an attempt to secure the first quantitative data on the degree and extent of this predation. The need for such a study has been emphasized by Lack (1954), and the work of Petrides (1956) has shown that correlations may exist between conditions in East Africa today and primitive conditions in North America.

The areas studied were in the Royal Nairobi National Park and the Royal Tsavo National Park in Kenya, and in the Serengeti National Park in Tanganyika. The park conditions provided the only sufficiently large concentrations of predators and prey to yield useful data in one field season. Data from the adjacent areas gathered by the field staff of the Tanganyika Game Department were included.

The main study areas were located after a preliminary reconnaissance at the end of the rains in June in Ngorongoro Crater in the eastern section of the Serengeti National Park, and in the watersheds of the Seronera, Orangi, and Grumeti Rivers in the western section. The two areas are separated by about 80 miles of waterless plain. Comparative game counts were run in Petrides' (1956) study areas in the Royal Nairobi National Park, and additional coverage was added in the dry bush country of the Royal Tsavo National Park 200 miles to the southeast. The areas sampled extended from Speke Gulf in the southeast corner of Lake Victoria to the Tiva and Galana Rivers in southeastern Kenya. This was an east-west distance of approximately 350 miles through some of the best game country remaining in Africa. The areas lie just south of the equator. Field work was begun in June and completed in October 1957.

The Seronera-Orangi-Grumeti drainage is the main water supply during the dry season for the large numbers of plains game in the western Serengeti Plains and acacia savannah, and lions and other predators concentrate along the rivers in numbers probably not surpassed elsewhere in Africa.

The predators studied were the lion, the leopard, the cheetah, and the East African wild dog, as primary killers of adult big game animals. The spotted hyaena, the black-backed jackal, and the baboon were also studied in their role as primary killers of the young of the large prey species, and as scavengers. Other predators are considered in the frequency with which their kills were found or reported to the study.

Nomenclature follows Swynnerton and Hayman (1950) for mammals, and Mackworth-Praed and Grant (1952) for birds. The reptiles follow Pope (1956). Scientific names are given at the end of the paper.

METHODS

The first operation on entering a new territory was the location of vulture roosts. These were the largest dead trees or stubs

[1] The study was supported by a grant from the North American Wildlife Foundation in cooperation with the Tanganyika Game Department, the National Parks of Tanganyika, and the Royal National Parks of Kenya. G. H. Swynnerton, Game Warden of Tanganyika, organized the field work in Tanganyika, and I am deeply indebted to him for advice and help on numerous occasions. Noel M. Simon, Assistant Director of the Royal Kenya National Parks, assisted the work materially in Kenya. To both I express my thanks.

in the area, and if none were available the largest living trees were used. Roosts were watched at first light and the direction vultures took in leaving the roost was noted. They were followed in the car to the nearest high point from which a lookout was available, and places where they were seen circling or landing were pin-pointed. In the savannah country, vultures landed on flat-topped acacias near a kill before going to the ground. When they were on the acacias they were very conspicuous to other vultures circling high in the sky, and thus appeared to relay to them the location of the kill. The vultures pitching down into the trees from high in the sky were seen from great distances by other vultures—and by watching biologists.

Vultures on the ground were always investigated, although their presence there did not always indicate a kill. In treeless areas they roosted on the ground, and they frequently gathered in groups around waterholes after drinking. Five species were noted in the course of this study. The commonest was the hooded vulture; the white-backed vulture, lappet-faced vulture, white-headed vulture, and Egyptian vulture made up the remainder.

Most game in the region came to the watercourses to drink during the night in the dry season. The predators, with the exception of wild dogs and cheetahs which hunted the open plains and savannah day or night, were concentrated along these watercourses about the favorite drinking places. They were therefore most easily located by cruising the watercourses rather than by hunting them in the open country beyond. Prides of lions were located by following a member found at the water back to the lying-up place, which was usually within half a mile. This was done early in the morning. Monkeys and baboons aided in locating leopards by climbing high trees and calling and staring in the direction of the animal's lying-up place.

The kills were usually found by the vultures shortly after first light about 6:30 a.m. (times of sunrise and sunset vary only about one-half hour in this latitude throughout the year). However, the predator had often not left the kill by first light. It was found by trial and error that 7:30–10:30 a.m. was the optimum time for kill examinations.

Lower jaws of all kills were collected when possible to determine the age of the prey. This material was placed in permanent storage at the museum of the Game Department of Tanganyika at Tengeru. No known-age series of jaws was available for comparison, so they were divided into age classes as follows: immature, young prime, prime, and past prime. Criteria were degrees of tooth wear and general appearance of the specimen. The physical condition of prey animals was judged from the state of the marrow in the round bones as either good or poor following Cheatum (1949).

The principal predators on big game were eight mammals ranging from the fox to the lion; the largest raptors; and two reptiles, the crocodile and the python. The principal food of foxes and jackals was small rodents, but they also preyed on the new-born young of the smaller gazelles as opportunity afforded. Baboons were mainly vegetarian and insectivorous, but they also turned carnivorous at times and attacked the helpless young of the gazelles. The extent of this predation was unknown, but since an actual instance was seen in the field, it was included here. The raptors which preyed on the young of the big game species were the crowned hawk eagle, Verreaux's eagle, the martial eagle, the African hawk eagle, and the bearded vulture or lammergeyer (Mackworth-Praed and Grant, 1952). The secretary bird has been observed to kill young Thomson's gazelles (Beaton, 1949).

Evidence of crocodile predation upon big game was difficult to obtain. The value of the hide has resulted in commercial hunting which has reduced the numbers so drastically that, except in protected areas, crocodiles were not important predators on big game.

OBSERVATIONS

Prey Populations

Estimates of prey populations are based upon strip counts run by car along roads

and tracks, and across country where possible. The failure of the car speedometer curtailed the work drastically in the western Serengeti, and the same type of count made by the Warden of the Western Serengeti, Mr. Myles Turner, for his monthly report was added to the study coverage. The width of strip varied from one-half mile on the open grasslands of the plains to 50 yards in the *Commiphora* scrub of Tsavo Park. The animals seen were divided into prey species and other animals.

The country of the western Serengeti is open grassland and savannah on which the predominant vegetation is trees and scrub of the genera *Acacia* and *Commiphora*. In Nairobi Park the country is the *Themeda-Acacia* grasslands (Edwards and Bogdan, 1951), with extensive areas of small whistling thorn (*Acacia drepanolobium*). The yellow-barked fever tree (*Acacia xanthophloea*) lines the watercourses. The greater part of Tsavo Park is waterless and uninhabited and covered with scrub of the genus *Commiphora*. This was the poorest habitat of the three for prey species of the large carnivora. Table 1 shows the stocking density of the prey species in these three habitats during July and August, 1957.

The table clearly shows the great difference in the densities of prey species in the region and points out the overwhelming superiority of the western Serengeti over any other area found. It should be pointed out that the census of the western Serengeti did not include the great herds of migrating wildebeeste and zebra which are impossible to count from the ground. None of my census areas were on the open plains because the great majority of the predators were in the savannah along the watercourses. Turner's (1957) censuses were run through savannah and plain at random, and were a cross-section of the country as a whole. The latest estimate of the number of large mammals (all major antelope species and zebras) in the Serengeti Park is about 370,000, but they are not confined to the Park all year. This estimate, made by M. Grzimek in 1957 and 1958 (Simon and Treichel, 1959; Grzimek and Grzimek, 1960), applies to an area of about 4,600 square miles.

I counted 91 Thomson's gazelles on one-quarter square mile on Seronera Plain in an area where the concentration was thinner than average. This was 364 per square mile, and the rest of the plain probably contained 400–500 per square mile. Several other species were also present in numbers.

TABLE 1.—STOCKING DENSITIES OF PREY SPECIES JULY–AUGUST, 1957, BASED ON STRIP COUNTS RUN BY CAR

Area and Observer	Cover Type	Area Sampled (Square Miles)	Stocking Density (Prey Animals per Square Mile)
WESTERN SERENGETI			
Wright	Savannah	2.2	500
Strip width ½ mi.	Savannah	2.3	322
	Savannah	1.2	500
	Savannah	1.1	920
Turner	Savannah and plain	5.5	395
Strip width ½ mi.	Savannah and plain	7.5	248
	Savannah and plain	16.0	Over 1,000
NAIROBI PARK			
Wright	Savannah and plain	15.0	61
Strip width ½ mi.			
Petrides (1953–1954)	Savannah and plain	11.0	120[1]
TSAVO PARK			
Wright	*Commiphora* scrub	4.6	24
Strip width 50 yds.			

[1] Petrides' Area A corresponds closely with the area censused in 1957. His result, adjusted to omit sheep and cattle, is given for comparison. The large difference in numbers of animals present may be due to the very late rains of 1957 which continued until the end of May, or it may be due to continued range deterioration since 1954.

TABLE 2.—SEASONAL VARIATION IN LION ABUNDANCE, ROYAL NAIROBI NATIONAL PARK (44 SQUARE MILES)[1]

Month and Year	Number of Days Reported	Total Lions Reported	Daily Average	Monthly Variation
1956				
July	22	284	13	4–9
Aug.	26	375	14	10–26
Sept.	27	402	15	10–21
Oct.	27	390	14	10–21
Nov.	26	355	14	5–23
Dec.	26	397	15	8–21
1957				
Jan.	31	466	15	10–22
Feb.	28	397	14	5–22
Mar.	30	467	16	6–27
Apr.	28	433	15	7–30
May	24	302	13	4–23
June	30	351	12	8–16
July	10	120	12	8–20
Totals	335	4,739		4–30[2]
Average			14	

[1] From park lion log. All known lions in the park are located daily with reference to topographical features or numbered posts accurately located on the park map. From this plot the daily total was worked out.

[2] Extremes

Predator Populations

The lion journals of Nairobi Park were studied to furnish information on the seasonal variation of the lion population. A summary of this information is given in Table 2. These journals are a daily record of the movements of all lions known to be in the Park, and are compiled under the supervision of the Warden.

It must be stressed that in certain areas lions, cheetahs, and wild dogs were migratory and followed the movements of the plains game. When on these migrations, the predators had a tendency to aggregate, and the stocking figures given here did not apply. However, another segment of the lion population appeared to be quite sedentary. The main lion prides in the Nairobi Park and about Seronera River in the western Serengeti were apparently year-round residents (Table 2 and Turner, verbal). It was not known whether the same lions were migratory at one stage of their lives and sedentary at another. The rates of killing and daily movements were computed from the sedentary prides, as they were the only ones that could be continuously observed. The period of study at Seronera River was after the peak plains game migrations had passed and the attendant migratory predators had moved on with them. The figures therefore approximated the sedentary predator populations of the area.

However, it should be pointed out that the migrations mentioned here were in no way comparable in distance covered to bird migrations. A circle of 200 miles diameter centered at Naabi Hill west of the crater highlands in the Serengeti Park would enclose most of the wildebeeste migrations, and the predators and other plains game were not known to move farther (Pearsall, 1957). Thus the predator-prey relationships within this area were considered as occurring within a more or less distinct ecological unit.

The concentrations of large predators that occur in the western Serengeti after the migrants had passed may be judged by the following observations. On August 15 an area of 2 × 2 miles was carefully covered by parallel strip counts. It contained 12 lions, 7 hunting dogs, and 1 leopard actually seen. This was 20 large predators on 4 square miles, not counting lesser predators and scavengers. On August 25, along the Orangi River, 15 lions were found in the 15 miles of river east of camp, and 4 in the 10 miles west of camp. Thus 19 lions were found in 25 miles, and 1 cheetah and a leopard; i.e., 21 large predators on 25 miles of river. This population could not be reduced to an area basis as the predators were concentrated along the rivers waiting for the game to drink. The game was drawn from many square miles of surrounding country.

The best available figures on the relative abundance of major predators in the eastern and western sections of Serengeti National Park were the estimates of Swynnerton (1957). In the eastern Serengeti, including the crater highlands forest, he rated lion, cheetah, and wild dog as less than 100 of each; in the western Serengeti, he rated lion, cheetah, and wild dog as between 100 and 1,000 of each, and leopard as less than 100.

The average size of a pride of lions was computed from 58 prides totalling 347 lions observed in the study, reported by the Game Department of Tanganyika, and recorded in the records of the National Parks. A pride was considered to be two or more lions of either sex travelling together, provided one was an adult. The average pride consisted of 0.8 adult males, 2.5 adult females, and 2.7 immatures, or a total of 6.0 lions. The largest pride seen in the study totalled 30 lions, 2 adult males and the remainder females and immatures of different ages.

Hunting circuits were regularly used but there was no evidence of defended territories. The prides in the Nairobi Park hunted the same general area without apparent friction, and on the Seronera River in the western Serengeti, a pride took possession of a waterhole and stayed beside it for several days, taking their prey from the animals coming to it. Then they disappeared completely for several days for no apparent reason, as the game was still coming to the waterhole, and reappeared at a new site a mile or more away.

Wild dogs travelled in packs varying in size from a single family of 5 to 7, to large groups up to 30. They were scattered over the region and had no particular concentration points, since they followed the migrations of the plains game. Cheetahs travelled in family groups, as pairs, and often singly. They also followed the plains game, concentrating on the smaller antelopes and gazelles. Leopards were solitary or in pairs, except for a mother with a dependent litter. They stayed close to cover, either in forest or rough ground, and remained on the same range all year round according to the Park Wardens.

The factors limiting predator populations are usually considered to be hunting by man, and the available food supply. Legal hunting is eliminated in the National Parks, and the best measure of the adequacy of the food supply is the reproductive rate of the population it supports.

When the Kruger National Park (then the Sabi Game Reserve) in South Africa was first established, a very high lion population was found in the area. In fact it had obviously passed the limit of the food supply because starvation was rampant within it (Stevenson-Hamilton, 1937). The reproductive rate was down to one or two cubs per litter, and the lions were hunting in prides of 20 or more. This gives a measure of the reproductive rate of a lion population that has passed the limit of its food supply.

The situation was so obviously desperate that despite the fact that the area was a game preserve, the lions were reduced by shooting. This produced an immediate change. The reproductive rate increased from one or two cubs per litter to four or five. More important still was the fact that of these four or five cubs born, all, or nearly all, survived (Stevenson-Hamilton, 1937). This is a measure of the reproductive rate of a lion population well within the limit of its food supply. If the food supply of the Kruger-Sabi area under primitive conditions was approximately the same as that of the Serengeti area in 1957, it offers an opportunity to measure the present state of the Serengeti lion population.

Data previously presented show that the average pride in the Serengeti area in 1957 contained 2.7 immatures. This was still above the one or two immatures in the Kruger-Sabi area at the time the food supply failed, but it was well below the four or five rate of the population within the limit of its food. This suggests that the Serengeti population may be approaching the limit of its food supply.

The average pride in the Serengeti area was 6.0 lions in 1957. This is still well below the 20 or more of the Kruger-Sabi area at the time of the overpopulation. However, there was one pride of 30 in Ngorongoro Crater that year. Particularly in the small area of the crater (approximately 160 square miles) is an overpopulation liable to develop. There were counted and estimated to be at least 70 lions, mostly females and cubs, in the crater in August 1957. It was noticeable that the wildebeeste and zebra were to be found on the short grass plains where they were difficult to approach, and the stream from which they drank ran through

the short grass so the game did not have to enter the long grass. In one hunt observed, a pride of 30 lions was only able to kill one Thomson's gazelle in the long grass, although several hundred widebeeste and zebra were on the short grass half a mile away. In the western Serengeti, the watercourses were flanked with belts of long grass, and lions killed wildebeeste and zebra regularly. Thus the vulnerability of the main prey species was greater in the western Serengeti than it was in the crater, as the same species were involved in both areas.

Mortality among Predators

Leopards were regularly hunted by poachers because of the high price of the pelt. They and the crocodile were the predators whose numbers have been most seriously depleted by man in recent years. The removal of the leopard as a controlling factor on baboon populations has resulted in serious losses from baboons in some areas. Reintroductions of leopards have been carried out to meet the menace in Kenya. They are live-trapped in farming areas where they are undesirable and released in baboon-infested areas (Kenya Wild Life Society, 1957).

Wild dogs were occasionally preyed upon by leopards (Beaton, 1949). Their general ferocity and pack tactics usually insured them from molestation by other predators despite their relatively small size. A single female, weighing not more than 35 pounds, was seen three times to drive off a hyaena several times her size by simply walking towards it in a fighting attitude.

In the Rungwa River Reserve two separate lionesses were found that had been killed by elephants (Tanganyika Game Department, Annual Report, 1957). One had its neck broken and the other its skull crushed, and they were both freshly killed when found by the Game Ranger with elephant tracks about the carcasses. As numbers of smaller game were using the same waterholes, it was difficult to see why they should attack elephant. Since an elephant could not catch a lioness that did not close with it, it seems probable that the lionesses attacked the elephants when they came to the waterhole.

Inter-specific strife among predators also operated as a minor mortality factor. A cheetah was surprised asleep and killed by lions in the Nairobi Park, and a caracal was killed by a python (Warden Ellis verbal, and Beaton, 1949). Hyaenas were particularly liable to this type of mortality, as they were frequently caught and killed by lions defending their kill. A black-backed jackal was also found killed by a leopard. These instances were exceptional but happened often enough to warrant mention in any discussion of predator mortality factors.

Life of a Pride of Lions

The most important single predator on the large land mammals of East Africa was the lion. An opportunity to gather first-hand information on the life history of this predator was presented by a pride of lions consisting of two lionesses and eight cubs in the Royal Nairobi National Park. Since the birth of the cubs, their daily movements had been recorded in a journal maintained at the park headquarters under the supervision of the Warden. They were completely wild, and their movements were restricted in only one direction (toward the city of Nairobi) by a fence. They were living on the game of the Athi Plains, which is typical of the region.

The journal showed that the cubs were born as a litter of four to the first lioness on September 10, 1955, and a litter of four to the second lioness on December 13, 1955. There were five males and three females among the cubs. The two litters were first seen travelling together as a pride on December 27, 1955, and they were still together on July 10, 1957, when a second pride of eight was found in the park and the movements of the two became confused. I plotted their daily movements during this period, and the distances of the nightly hunts was approximated by measuring the distance between lying-up places. A summary of this unique record is shown in Table 3.

The first point of interest in this table was the relationship it showed between the

TABLE 3.—NIGHTLY MOVEMENTS OF A PRIDE OF TWO LIONESSES AND EIGHT CUBS[1]

Age of Youngest Litter (Months)	Total Nights Observed	Number Nights Moved	Percent Nights Moved	Nightly Move (Yards)	
				Avg.	Max.
2	31	12	39	2,600	4,000
4	60	31	52	2,100	6,000
6	60	42	70	1,900	5,000
8	59	40	68	2,400	5,000
10	41	29	71	2,300	4,000
12	45	32	71	2,300	4,500
14	52	39	75	3,100	7,500
16	51	30	59	2,500	6,000
18	41	29	71	2,900	10,000
20	27	24	89	2,800	6,500
Total	467	308			
Average			66	2,500	

[1] Compiled from the Nairobi Park lion log. This pride was located daily by game scouts and the park wardens and the lying-up points were recorded. These were plotted and the movements measured. The period covered was September 10, 1955–July 10, 1957.

age of the youngest cubs and the nightly range. When the youngest cubs were two months old the pride was moving an average of 2,600 yards on the nights they hunted, and might move as far as 4,000 yards. This was as large a nocturnal movement as they would average in the first 20 months of their lives. At 6 months they were moving an average of 1,900 yards, with a maximum of 5,000 yards per hunt. This gradually increased to an average of 3,100 yards and a maximum of 10,000 yards in the next 14 months. This requirement for very young cubs to travel as far at 2 months as at 20 months was significant. It was noted by the Warden of Nairobi Park that small cubs were not infrequently lost by drowning when trying to follow their mothers across rivers in flood.

When the youngest cubs were 6 months old, the pride was hunting 7 nights out of 10. The frequency of hunts increased to almost 9 nights out of 10 by the time the youngest cubs reached 20 months of age.

The annual range of this pride was enclosed in a roughly rectangular area 8.7 × 3.8 miles, or 33 square miles. This area was also hunted over by several other prides, all smaller than the one under study. The hunting circuit of two previous prides had been observed by Beaton (1949) in this area. The first circuit was about 46 miles in length, and the second about 80 miles. He further stated . . . "At times they will split up into smaller parties and hunt in opposite directions. Sometimes, for no apparent reason, a pride will suddenly leave a locality altogether and move to another area up to twenty miles away." (Page 94). The pride under study had remained 20 consecutive months on the same range, and was on the point of breaking up as a pride at the end of this time. As a hunting unit it lasted for approximately 2 years, all of which was spent in an area of 33 square miles. It would break up when the adult females accepted mates again and these mates drove off the male cubs of the present litter. The female cubs were presumably accepted into the harems of the adult males.

Old females which have passed the breeding age were known as "aunties" by the hunters, and their function was that of baby-sitters to the young breeding females. The only time I could claim to have been attacked in the course of this study involved one of these "aunties." I had driven up a hill in Ngorongoro Crater and was approaching the top. As I was slowing to a stop, a lioness came for the car without warning from the long grass about 25 yards away. It was necessary to drive at 40 miles per hour to outrun her. She was within 5 yards of the tail board of the open car most of the way. She had one blind eye and every appearance of old age.

Six weeks later I again drove up this hill. I was not molested, but I nearly ran over a litter of lion cubs in the grass. They were estimated to be 6 weeks old, so my previous visit had been either just before or just after their birth, and the old female was standing guard.

Litters varied from two to six with an average of four (Beaton, 1949). The cubs were born with the eyes open, but they could see very little for the first few days. Their diet was entirely milk for the first two months. They were weaned on meat regurgitated by the female, and passed on

TABLE 4.—SEX, AGE, AND CONDITION OF PREDATOR KILLS

Predator	Sex			Age					Condition		
	Total Sexed	Male	Female	Total Aged	Immature	Young Prime	Prime	Past Prime	Total	Good	Poor
Lion	49	29	20	76	9	9	38	20	28	25	3
Leopard	3	1	2	7	4	1	2	–	5	5	–
Cheetah	4	4	–	7	2	3	2	–	4	4	–
Wild Dog	4	1	3	3	–	2	–	1	–	–	–
Spotted Hyaena	–	–	–	2	2	–	–	–	–	–	–
Baboon	1	1	–	3	3	–	–	–	–	–	–
Python	1	1	–	–	–	–	–	–	1	1	–
Black-backed Jackal	–	–	–	1	1	–	–	–	1	1	–
Crocodile	1	–	1	–	–	–	–	–	–	–	–
Secretary Bird	–	–	–	1	1	–	–	–	–	–	–
Unidentified	4	3	1	5	–	–	2	3	4	4	–
Totals	67	40	27	105	22	15	44	24	43	40	3
Percentage	100	60	40	100	21	14	42	23	100	93	7

Note: This table does not include the 96 kills which were identified to species only when evidence of sex, age, and condition was missing. It includes only those 115 kills in which evidence of any, or all, of these qualities was present. Evidence of sex was present in 67 kills; of age in 105 kills; and of condition in 43 kills.

to lumps of fresh meat brought to them from a kill (Beaton, 1949). Drowning as a mortality factor has been mentioned, but a more serious one occurred between the ages of 1 and 2 years. Then the mother's care was waning and the cubs had to fend for themselves. Many weaker cubs died at this time because of their inability to compete with stronger members of the litter for adequate food (Beaton, 1949).

The females of the pride under study were accompanied by adult males at the twentieth month. The immature males were still tolerated by the adult males, but as soon as they reached sexual maturity (they had not at the time of observation) they would be driven off or killed.

Predator Food Habits and Hunting Methods

The field staff of Royal Kenya National Parks at the Nairobi Park under Warden Ellis, and the records of the former Warden of this Park, K. de P. Beaton, reported 44 kills to the study. The Wardens of the Eastern and Western Serengeti National Park in Tanganyika, Mr. Harvey and Mr. Turner respectively, reported 41 kills. The Tanganyika Game Department's District Rangers reported 16 kills. Mr. T. O. Mathews, professional hunter for Ker and Downey Safaris Ltd., reported 2 kills. The remaining 108 kills were examined by me. These 211 kills were combined for the purpose of analysis.

Table 4 shows that predators were killing more males than females in the ratio of 60:40. Animals in the prime of life and in old age made up 65 percent of the predator kill, and the overwhelming majority (93 percent) were in good health. Nicholson (1947) has suggested that when this situation exists the limiting factor on the predator population is not the food supply of the prey, but the means by which it escapes, involving questions of space and cover.

Lion.—The main food supply of the lion in the region studied was wildebeeste, zebra, and Thomson's gazelle. These three made up 74 percent of all lion kills (Table 5). Adult wildebeeste in the prime of life and in old age were the age classes taken, and most of them were in good condition. This was different in the zebra, where immatures and old animals were the age classes found in the kill sample. Thompson's gazelles were mainly adult animals, with a distinct preponderance of males. The age classes of all prey killed by lions showed that immature and young prime animals were to prime and past prime animals as 24:76.

A typical lion hunt was observed in

TABLE 5.—ANIMALS KILLED AND EATEN BY LIONS IN SOUTHERN KENYA AND CENTRAL TANGANYIKA

	Total Kills	Percentage
PREY SPECIES		
Wildebeeste	73	49
Zebra	22	15
Thomson's Gazelle	15	10
Buffalo	7	5
Giraffe	6	4
Impala	5	3
Kongoni	3	2
Eland	3	2
Ostrich	1	tr.
Grant's Gazelle	1	tr.
Topi	1	tr.
Porcupine	1	tr.
Tortoise	1	tr.
Hippo	1	tr.
Bush Pig	1	tr.
LESSER PREDATORS AND SCAVENGERS		
Spotted Hyaena	5	3
Black-backed Jackal	3	2
Cheetah	1	tr.
Totals	150	
Percentages		100

Ngorongoro Crater. The lionesses came out of the reeds where the pride was lying up in the middle of the afternoon and spread out in the grass and lay down. The combined stalk started when the prey animals grazed within striking distance of where the predators were lying. They seemed to spend as much time waiting for the prey to feed up to them as they did in trying to stalk it. When they moved in the 2-foot-high grass, they walked with heads low in a sway-backed slouching gait which showed nothing above the grass. Each lioness in the hunting team raised her head individually to look at the game; rarely were two heads up together. They moved ahead 20 yards at a time and lay down, moving one at a time.

When six lionesses were in the hunting team they were in crescent formation 50 yards across, about 375 yards from a mixed herd of Thomson's gazelles and a few zebras. The crescent gradually moved toward the feeding herd, and in one hour it moved forward only about 100 yards. By 5:15 p.m. the light was beginning to fail and the hunting team was still 250 yards from the herd. Meanwhile two adult males and a large number of cubs of various sizes had come out of the cover and were lying in the dying sun watching the lionesses. A total of 30 lions was in sight. The cubs began to follow the lionesses, and several about one-third grown joined the hunting crescent. When darkness closed the observation there were nine lionesses and cubs in a crescent 175 yards across moving up on the herd. Next morning a Thomson's gazelle kill, with a lion-killed hyaena beside it, was found about 300 yards from where the lions were last seen the evening before.

When the lionesses have made the kill, the males come forward and appropriate it. Only when the males have finished eating do the females and cubs make their meal. Under this system, when kills are small and few as in this instance and adult appetites are keen, there is little left for the cubs.

Leopard.—Fifteen leopard kills were recorded, of which seven were Thomson's gazelles, two each were wildebeestes and impalas and one each was a zebra, baboon, wild dog, and an unidentifiable herbivore (probably another Thomson's gazelle. Both the wildebeestes and the zebra were immature animals. The Thomson's gazelles were adults in good condition. The effect upon the baboon population of the reduction of leopards has already been mentioned. Illegal poaching was apparently the sole reason for the shortage of leopards.

Wild Dog.—Ten wild dog kills were recorded, of which seven were Thomson's gazelles, and one each was a wildebeeste, a reedbuck, and an impala. The Thomson's gazelle was the staple diet of the pack studied on Seronera Plain, which was a family of two adults and four pups.

A typical hunt was observed on Seronera Plain. The female cantered off across the plain, leaving the male with the four pups walking slowly behind. The game scattered ahead of her and she passed quite close to several groups of Thomson's gazelles without deviating from her course. Two hundred yards ahead and directly in front of her a Thomson's gazelle turned and ran on

the same course the dog was following with the curious gait known as "stotting," in which all four feet strike the ground together. This was the one gazelle that was panic-stricken at the sight of the approaching dog, which immediately centered her attention on the gazelle. The dog broke into a gallop, passing through a closer group of gazelles, to follow the animal that had started to run before the dog was close.

The gazelle was between one and two hundred yards ahead, bounding along without apparent effort or fright. The dog was still at a steady gallop. The gazelle began to circle the plain and the dog narrowed the gap by cutting across the arc, and closed to about one hundred yards. The gazelle still did not appear excessively frightened and was still bounding along well within the limit of its speed. The chase had now continued for about 2 miles in a half-circle. During this period the pups had lain down in the grass and the male had left them and was lost to sight. Suddenly, as upon receiving a signal, the female increased her speed to the utmost, and the now startled gazelle bounded ahead with frequent glances behind. When its attention was concentrated upon the pursuing dog, the male rose from the grass within 10 feet of the gazelle as it passed. He was beside it in one bound and laid open its flank just behind the ribs with one slashing bite. This knocked the gazelle to the ground, and the dog thrust his head into the wound to the ears and jerked backward with all his weight, carrying with him almost the entire contents of the body cavity. The pups then joined their parents at the kill.

Other Predators.—Twelve cheetah kills consisted of seven Thomson's gazelles, three impalas, and one each of wildebeeste and Grant's gazelle. The wildebeeste was an immature animal. The spotted hyaena was recorded as the killer of two Thomson's gazelles, one an immature, and a young African hare. The black-backed jackal was responsible for the death of one young Thomson's gazelle and a dikdik, and a baboon was caught in the act of devouring a young Thomson's gazelle. Baboons are commonly believed to prey on young gazelles, and one was seen carrying a carcass and was chased with the car until it dropped what proved to be the remains of a freshly killed young gazelle.

A python was recorded as having killed an adult male Thomson's gazelle in good condition, a duiker, and a caracal (Ellis, verbal; Beaton, 1949). A crocodile killed a doe impala, and a caracal killed another impala (Beaton, 1949).

Four Thomson's gazelles, including two males in the prime of life and in good condition, were killed by an unidentified predator. Also unidentified was the predator that killed three old zebras and a black-backed jackal, but this was probably the work of a lion or leopard. Positive identification could not be made because there was not enough left of the prey.

Relation of Predators to Scavengers.—Lions and leopards frequently killed and sometimes ate the scavengers that followed them. Lions would spend hours chasing vultures off their kills. On one occasion near Banagi a pride of 11 lions killed an old bull giraffe. They fed on the kill from June 6–June 8, going in relays to the river to drink and leaving one member of the pride behind to keep scavengers from the kill (Turner, verbal). Lions will also rob a leopard of its kill if the prey is too heavy for the leopard to carry up a tree.

Vulnerability of the Prey Species

Thomson's gazelle, the most widely utilized prey species, was preyed upon by 9 of the 11 identified predators, and by the unidentified predators. The majority of specimens killed were males in the prime of life or in youth, and all were in good condition.

Seven predators preyed upon impala, although it is comparatively few in numbers. It is an animal of the scrub and savannah where predators concentrate during the dry season, and where hunting conditions are at their best.

More wildebeeste kills were found than Thomson's gazelles, although it was preyed on by only four predators. It was thus rated third in importance as a food animal.

TABLE 6.—THE RELATIVE VULNERABILITY OF PREY SPECIES

	Recorded Predators	Total Kills
PREY SPECIES		
Thompson's Gazelle	10	47
Impala	7	14
Wildebeeste	4	77
Zebra	3	28
Grant's Gazelle	2	2
Buffalo	1	7
Giraffe	1	6
Kongoni	1	3
Eland	1	3
LESSER PREDATORS AND SCAVENGERS		
Black-backed Jackal	2	4
Caracal	1	1
Spotted Hyaena	1	5
Cheetah	1	1
Wild Dog	1	1
Total		211[1]

[1] Recorded once each among the predator kills were Topi, Duiker, Ostrich, Hippo, Reedbuck, Bush Pig, Dikdik, African Hare, Porcupine, Tortoise, Baboon, unidentified herbivore.

However, this difference in number of kills was more apparent than real, since all traces of a Thomson's gazelle kill could be obliterated much more quickly and easily than those of a wildebeeste, and for this reason wildebeeste kills were more easily found. Both species were equally available to predators. There was a slight preponderance of females in the wildebeeste kill, mostly at or past their prime. Their condition again was usually good.

Zebras were utilized by only three predators, but the frequency with which they were taken made them fourth in importance as a food animal. The sample indicates that young and old were more frequently taken than adults in their prime. Sex was difficult to determine in most specimens, as identifying parts were consumed either by the predator or by scavengers.

Predation on Thomson's gazelle, impala, wildebeeste, and zebra, was continuous and heavy, and only sporadic on the other species listed in Table 6. It follows therefore that predator populations will be influenced more profoundly by changes in populations of these four than in any of the others, as there are no other alternative prey species in equivalent numbers. Wildebeeste, zebra, and Thomson's gazelle are plains game depending on conditions of water and grazing. These factors are far less important to the impala, which live in the scrub.

Rate of Killing by Lion Prides

The rate of killing by lions in prides was computed from the records of three prides. The first, a pride of four adults with one small cub hunting large game, was killing at the rate of 243 kills per year. The second, a female with dependent yearlings hunting medium-sized prey, was killing at the rate of 305 kills per year. The third, two females with eight well grown cubs hunting large game, was killing at the rate of 110 kills per year. In comparison a pack of wild dogs, hunting Thomson's gazelles almost exclusively, was killing at the rate of 281 kills per year. The first and second lion prides and the wild dogs were hunting in the western Serengeti. The third lion pride was hunting in Nairobi Park, where prey animals were much less abundant.

The relation between food provision rate and the total weight of the predators consuming the food was computed for the same prides of lions and the wild dog pack. The first pride killed 0.13 lbs. of food per day per pound of lion in the pride. The second killed 0.11 lbs., and the third 0.11 lbs. The wild dogs killed 0.15 lbs. per day per pound of dog in the pack, and showed themselves to be as effective predators as the lions in proportion to their size. The weights of predators and prey were estimated from known weights available from the Tanganyika Game Department, the records of Mr. Carr Hartley, animal dealer of Nairobi, and from captive specimens. These records indicated a uniform rate of food provision by the major predators of 1–1½ lbs. of food per day per 10 lbs. of predator. This was the rate for predators living and hunting communally. Single predators would greatly exceed this rate when hunting big game in Africa, as their individual kills would be well beyond their capacity to consume before being cleaned up by scavengers.

The food requirements of an adult lion in captivity are 35–40 lbs. every second day, or an average of approximately 20 lbs. per day maximum (Carr Hartley, verbal). The rate of killing in the wild by the pride of adults was 0.13 lbs. per day per pound of lion. This was 45 lbs. of food killed per day by the average adult lion of 350 lbs. living in a pride. Thus wild lions were apparently killing twice as much food as they themselves required, and the surplus fed the scavenger population. In other words, lion predation appears prodigal of its food supply. However the ratio of required food between wild and captive lions is unknown, and this surplus may be more apparent than real.

A reduction of the scavenger population to allow the lions a second meal from a kill should be tested as a management measure in areas where lions have reached the limit of their food supply, and where it is desired to maintain a high lion population at the expense of scavengers. Prodigous use of food was also true of the cheetah to a lesser extent, but not of the leopard, which cached many of its kills in trees to avoid land scavengers. Wild dogs travelling in moderately large packs left little for scavengers of any but the largest kills.

Annual Consumption of Prey

The annual kill of prey animals by the average lion pride in the region was computed from data on hand. The average pride, consisting of an adult male, two adult females, and three immatures (decimals from page 5 rounded off to whole numbers), made 219 kills in a year if they conformed to the average rate of killing of the three prides studied. Table 5 shows that 49 percent, or 107, were wildebeestes; 15 percent, or 33, were zebras; 10 percent, or 22, were Thompson's gazelles; and the remaining 26 percent, or 57 kills, were miscellaneous prey animals and scavengers. These 219 prey animals could be carried on 3.9 square miles of the *Themeda-Acacia* areas at the average densities found by Petrides (1956) in 1953–1954, and on 7.8 square miles at densities found in 1957. In the western Serengeti during the migrations there were often sufficient prey animals to sustain this average pride for a year on one-half square mile, but these densities were not sustained throughout the year.

Relation of Predation to Soil Erosion

Predation is directly linked to the most important land use problem in East Africa today—the destruction of range by erosion, following overgrazing and trampling by massed herds of native cattle. When overlooking a plain in East Africa, an observer could tell cattle from wild game even though both were too far off to distinguish characteristics. The game was spread over the plain evenly as a sprinkling of black dots, but the cattle were closely packed masses of animals with the appearance of large black blobs.

Cattle rarely spread out, even when left unattended by herd boys. This seldom happens, as it is a capital offense on the part of herders. Cattle are all wealth to the pastoral tribes, and a stray animal left out overnight will seldom escape predators. The plains game graze widespread over the range, using the tops of plants and not disturbing the roots with their wandering hooves, but cattle graze in massed herds, consuming plants down to ground level. Their hooves cut up the root mat and churn the loose volcanic soil. Wind erosion in the dry season, and water erosion in the wet season, quickly result in heavy gullying and complete destruction of the range.

This tendency to bunch has been bred into the cattle through generations of close herding. Thus the age-old competition between pastoral man and his herds and the predators has resulted here in destruction of the range upon which both man and predators depend.

DISCUSSION

The greatest single tourist attraction of Serengeti National Park is the lions for which the region is world famous. Their continued abundance in the area will depend upon the preservation of adequate sup-

plies of food in a habitat which is favorable to the hunting methods of the lion. Large numbers of prey animals on short grass plains will support fewer lions than a smaller number on broken ground with abundant cover. This study has indicated that the limiting factor on the predator population in the region may not be the food supply of the prey, but its vulnerability. Thus if it is desired to increase the predator population, at the cost of depressing the prey, the habitat should be managed to increase vulnerability of the prey. This would involve protecting belts of cover from fire along the watercourses, which is not done now.

The greatest, and perhaps only, management need of the leopard is protection from poaching. Its food supply and habitat are adequate to support a much higher population than now exists, and one of its main food animals—the baboon—has become a menace because of the release from leopard predation.

Cheetahs and wild dogs do not usually hunt at the waterholes, and the short grass plains are their normal hunting ground. The present practice of widespread burning of the grass is probably to their benefit.

Whether or not the net effect of predation on prey populations is to remove the surplus game above the limit set by the competitive balance between game and domestic stock in the area will require more detailed study. Errington (1956) has pointed out that predation as a mortality factor may be of little importance if the prey population level is set by another influence. In this case, such an influence might be range competition between game and native cattle and goats. Both Petrides (1955) and Talbot (1956) have stressed the disastrous effects of overgrazing and competition with domestic stock in the region, and Pearsall (1957) has recommended the early exclusion of pastoral occupation from the National Parks. If this recommendation is carried out, the effect of predation as a population depressant will be clearer. This study has indicated the relative importance of various prey species to predators, and points out where management effort must be concentrated to maintain the large predators as an essential part of the balance of species within the environment.

The relation of predation to soil erosion stresses the need for inviolate sanctuaries where the requirements of large predators can be given priority. This is becoming increasingly important as the human population of the area increases, if these species are to continue to exist as anything but scattered remnants.

SUMMARY

A study of food habits, hunting methods, and habitat requirements of the large predators was carried out in southern Kenya and central Tanganyika between June and October, 1957. The use of vultures to locate predator kills is described. Lower jaws of all animals killed by predators were collected and ages determined by degree of tooth wear and general appearance of the specimen. The condition of the animals killed was judged by state of the marrow.

Concentrations of large predators, as high as 20 on 4 square miles, were noted at Seronera River, and 19 lions were found along 25 miles of the Orangi River. The average-sized lion pride was found to be 6.0 lions. The rate of survival of the young indicates that the Serengeti lion population may be approaching the limit of its food supply.

Leopards and crocodiles were greatly reduced in numbers by legal and illegal hunting. Baboons have become a pest in some areas following release from leopard predation. Reintroduction of leopards has been started in Kenya.

The life of a lion pride is followed for 20 months. Mortality factors among the young are competition for food and drowning. Individual nightly hunts of a pride may cover as much as 10,000 yards. The annual range of one pride was 33 square miles.

Food habits of large predators were studied in a sample of 211 kills. The predators were killing more males than females, and more animals in the prime of life and in old age than young animals. Most prey

COMMON AND SCIENTIFIC NAMES

PREDATORS AND SCAVENGERS	
Mammals	
Lion	*Panthera leo massica* (Neumann).
Leopard	*Panthera pardus fusca* (F.A.A. Meyer).
Cheetah	*Acinonyx jubatus* (Schreber).
Caracal	*Caracal caracal nubicus* (J. B. Fischer).
East African Wild Dog	*Lycaon pictus lupinus* Thomas.
Spotted Hyaena	*Crocuta crocuta* (Erxleben).
East African Black-backed Jackal	*Canis mesomelas mcmillani* (Heller).
Baboon	*Papio anubis neumanni* Matschie.
Birds	
Crowned Hawk Eagle	*Stephanoaetus coronatus* (Linnaeus).
Verreaux's Eagle	*Aquila verreauxii* (Lesson).
Martial Eagle	*Polemaetus bellicocus* (Daudin).
African Hawk Eagle	*Hieraaetus spilogaster* (Bonaparte).
Bearded Vulture (Lammergeyer)	*Gypaetus barbatus* (Linnaeus).
Secretary Bird	*Saggittarius serpentarius* (Miller).
Hooded Vulture	*Necrosyrtes monachus* (Temminck).
White-backed Vulture	*Pseudogyps africanus* (Salvadori).
Lappet-faced Vulture	*Trogos tracheliotus* (Forster).
White-headed Vulture	*Trigonoceps occipitalis* (Burchell).
Egyptian Vulture	*Neophron percnopterus* (Linnaeus).
Reptiles	
Crocodile	*Crocodylus* sp.
Python	Pythoninae sp.

PREY SPECIES	
Mammals	
Wildebeeste	*Gorgon taurinus hecki* (Neumann), and *Gorgon taurinus albojubatus* (Thomas).
Zebra	*Equus burchelli bohmi* Matschie.
Thomson's Gazelle	*Gazella thomsonii thomsonii* Gunther.
Buffalo	*Syncerus caffer caffer* (Sparrman).
Giraffe	*Giraffa camelopardalis tippelskirchi* Matschie.
Impala	*Aepyceros melampus suara* (Matschie).
Kongoni (Hartebeeste)	*Alcelaphus buselaphus cokii* Gunther.
Eland	*Taurotragus oryx pattersonianus* Lydekker.
Grant's Gazelle	*Gazella granti granti* Brooke, and *Gazella granti serengetae* Heller.
Topi	*Damaliscus korrigum jimela* (Matschie).
Porcupine	*Hystrix galeata conradsi* F. Muller.
Hippopotamus	*Hippopotamus amphibius amphibius* Linnaeus.
Bush Pig	*Potamochoerus porcus daemonis* Major.
Duiker	*Sylvicarpa grimmia* (Linnaeus).
Reedbuck	*Redunca redunca* (Pallas), and *R. fulvorufula* (Afzelius).
Dikdik	*Rhynchotragus kirkii thomasi* Neumann.
African Hare	*Lepus victoriae victoriae* Thomas.
Birds	
Ostrich	*Struthio camelus massaicus* Neumann.
Reptiles	
Tortoise	Genera *Kinixys* and *Homopus*.

animals killed were in good condition. Thomson's gazelle, impala, wildebeeste, and zebra were the most widely used prey animals, in that order.

The large predators were found to have a rate of food provision of 1–1½ lbs. of food per day per 10 lbs. of predator. Lions, prodigal with their food supply, were supporting a large scavenger population. A reduction of the scavenger population to allow the lions a second meal from a kill is suggested as a possible management technique.

The massing of natives' cattle for protection against predators is a major factor in causing soil erosion by overgrazing.

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THE ROOSEVELT ELK ON AFOGNAK ISLAND, ALASKA

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Prior to 1921, the only big game animal indigenous to the Kodiak Island group was the Kodiak bear (*Ursus middendorffi*). Big game animals introduced to the Islands in recent years have been: deer (*Odocoileus hemionus sitkensis*), 1924, elk (*Cervus canadensis roosevelti*), 1928, and mountain goats (*Oreamnos kennedyi*), 1952.

This paper reports the success of the introduction of the Roosevelt elk, their present population and distribution, local habits and characteristics, and the hunting harvest.

HISTORY OF INTRODUCTION

In 1928, eight elk calves, consisting of five females and three males, were transplanted from the Olympic Peninsula in Washington to Kalsin Bay on Kodiak Island. They were kept in a semi-domesticated state throughout the first winter. However, because of the conflict with a local grazing enterprise, they were transplanted to Afognak Island in the spring of 1929. No additional introductions were made and the present population stems from this small plant.

DESCRIPTION OF THE AREA

Afognak Island lies within the Kodiak Island group and is located 3 miles northeast of Kodiak Island (Fig. 1). It extends approximately 37 miles northeastward and averages 24 miles in width. The total land area of the island is 780 square miles and it is deeply indented with bays. Raspberry Island, mentioned in this paper, is considered part of Afognak Island, as it is connected by land on low tides.

The island topography is one of gradual sloping mountains rising from 1,000 to 2,000 feet in elevation with a lowland in the central portion. The two major vegetative types are climax spruce forest and brush. The central portion is covered with a dense climax spruce forest (*Picea sitchensis* (Bong) Carr). In the mountain areas the spruce line often reaches 1,200 feet. The understory consists primarily of blueberry (*Vaccinium ovalifolium* Smith), devil's club (*Oplopanax horridus* (SM.) Miquel), salmonberry (*Rubus spectabilis* Pursch) and some elderberry (*Sambucus racemosa*). In the western

FIG. 1.—Afognak Island.

(Raspberry Strait) area and the eastern (Tonki Cape) area, the climax spruce forest is found only in the lowlands and is not continuous. Large portions of these two areas are covered with land growth of brushy vegetation consisting of alder (*Alnus fruiticosa* Rupr.), willow (*Salix* spp.), elderberry and salmonberry, interspersed with open grassy areas, consisting primarily of bluejoint (*Calamagrostis canadensis* (Michx) Beauv.) and fireweed (*Epilobium angustifolium* L.).

Temperatures are mild, seldom dropping lower than 10 degrees above zero and rarely exceeding 80 degrees. The island receives an average annual precipitation of 60 inches, most of it in the form of rain, especially during spring and fall months. Snowfall is the heaviest from December through March and sometimes exceeds 90 inches. Periodic rains during winter months often keep the lower elevations and seacoasts fairly free of snow.

POPULATION AND DISTRIBUTION

Little data are available on population increases in the early years after the introduction. In 1941, 64 animals were counted in the Raspberry Strait area by U.S. Game Management Agent Jack Benson; he estimated the total population at 147. In December, 1948, Urban C. Nelson and David L. Spencer completed an aerial census and tabulated 116 animals. They estimated the total population at 212 elk (Nelson, 1949). Since 1951, an annual aerial census has been flown during the summer or early fall months when most elk are found on the higher open slopes and are easily visible. Total numbers observed have gradually increased as shown in Table 1. In 1958 the actual population count was 599 and the total population is now estimated to be 800 elk.

About 20 percent of the elk population is found on Tonki Cape and the remainder in Raspberry Strait. Only occasional stragglers get into the central portion of the island.

A few small islands dot the channel separating Afognak and Kodiak Islands. Elk can cross from Afognak to Kodiak Island by swimming a channel less than 1 mile wide. A few elk have been seen on the larger island, but to date a resident population has not become established. A portion of Kodiak has habitat similar to that of the Raspberry Strait area, and elk may eventually become established on this island.

HERDING TENDENCIES

The Roosevelt elk on Afognak are un-

TABLE 1.—ELK POPULATION AS DETERMINED BY SURVEYS AND ESTIMATES ON AFOGNAK ISLAND

Year	Actual Count	Estimated Population[1]
1929	8	8
1941	64	147
1948	116	212
1949	161	–
1951	264	–
1952	345	–
1953	152[2]	–
1954	408	–
1955	273	450
1956	345	450
1957	456	600
1958	599	800

[1] Estimates based on known populations in certain areas not covered by the survey.
[2] Survey not complete.

usually gregarious. Large herds are a common occurrence rather than an exception. In western Oregon, herds seldom exceed 50 animals (Graf, 1955: 17). In the Olympic region of Washington, herds sometimes reach several hundred animals (Schwartz and Mitchell, 1945), but they apparently do not remain grouped for long periods of time.

On Afognak, elk remain in large herds during the greater part of the year. Just prior to calving time elk groups are loosely formed. By late June cows and calves have banded together in groups of 50 to over 100 animals and by July are joined by a few bulls, especially spikes. Groups of 4 to 20 bulls often band together during the spring and early summer, and at this time lone males are occasionally seen. These have a tendency to remain at the lower elevations. Prior to and during the rut, bulls merge with the bands, at which time the bands are usually the largest.

During the rutting season in September, 1958, the elk population on Afognak consisted of five major herds listed below:

Raspberry Island	137
Malina	144
Upper Raspberry Straits	137
Lower Raspberry Straits	69
Tonki Cape	112

A few days after the survey was flown, the lower Raspberry Strait herd numbered 112 animals rather than 69, indicating that a portion of the herd was missed in the first count.

Bulls gradually drift away from the bands after the rut. Large herds often remain essentially intact throughout the winter and do not become scattered until just prior to the calving season. There is some tendency for herds to become smaller in winter months, a characteristic more pronounced during winters of heavy snows.

MOVEMENTS

Because of the small size of Afognak Island, elk do not travel any great distance between winter and summer ranges. During most of the summer and into early winter, elk feed on the open slopes above timberline; however, they may also be found in the lowlands during this period. After heavy snows, elk remain at the lower elevations in or near spruce timber. As snows recede during spring, they return to higher elevations.

Two herds, the Raspberry Island and Malina, summer along the northwestern shores where the range is primarily a climax vegetation of alder and willow, interspersed with grasses. These herds migrate to the summer ranges in May and June and remain until early winter. After heavy snowfalls they move southeastward into the spruce timber. The distance covered is rarely over 10 miles. Apparently spruce is desired at this time for the extra cover it provides. Snow depths under the spruce are less and movements are less restricted.

RUTTING PERIOD

Bugling starts in early September and continues through early October. Most breeding activity occurs in the last two weeks in September. At this time the elk on Afognak are still banded together in large groups. Contrary to observations made in other areas, one seldom sees a solitary bull guarding a harem of 15 to 20 cows.

On September 26, 1957, from a distance of 400 yards the author observed a band of 121 animals composed of 76 cows, 20 calves and 25 bulls. The latter were fairly evenly distributed throughout the band. A few of the larger bulls attempted to keep some of the smaller bulls at a distance by short threatening runs and prods, but they did not appear to be entirely successful. During this activity almost constant bugling could be heard. Two cows were bred while the herd was being observed.

On September 16 and 17, 1958, a band of 150 individuals was under observation for several hours each day in a lowland valley. Because of scattered spruce they could not all be seen at the same time. Bugling was almost constant and sparring activities between bulls, scattered throughout the band, could readily be observed. While under observation, 10–12 cows were bred. This usually occurred when a bull managed to single out a cow on the outskirts of the band.

CALVING

The major calving period is during early June. Calf tracks have been observed as early as May 23. In 1957, 23 cows were checked on June 5 and no calves could be found. On June 7 the same area was checked and of 28 cows observed, 5 had calves. This would indicate that calving was just starting.

In most areas, cows calve at lower elevations in spruce timber; however, the Malina herd calves on the open grassy slopes of their summer range.

FOOD PREFERENCES

Information on food preferences has been gathered by analysis of a limited number of stomach samples and by examination of areas recently grazed by elk.

As observed in other areas, the elk on Afognak are versatile feeders but depend on a few abundant forms of browse, grasses, ferns and weeds. Forage plants vary with the season and availability. The parts of plants taken also vary with the seasons. During summer and early fall the leaves of elderberry constitute a large portion of the diet. Fireweed and grasses are also grazed quite heavily. The contents of nine stomach samples collected during a September hunting season are given below:

Species	Occurrence	Percentage of Total Volume
Elderberry leaves (*Sambucus racemosa*)	9	58.0
Fireweed (*Epilobium angustifolium*)	9	33.0
Grasses (Gramineae)	5	9.0

Few observations are available from late April through June, but grasses and sedges are probably important sources of food during these spring months. During winter months willow and elderberry are the most important browse species and constitute the bulk of the food consumed. Considering the overall range, willow is by far the most important winter food taken; however, in a few areas where willow is not too abundant, elderberry becomes the number one browse. Blueberry and salmonberry are considered important browse plants in the Olympics (Schwartz and Mitchell, 1945) but are seldom utilized on Afognak. Even when traveling through areas where very little other browse is available, elk seldom touch these two species.

In late winter the terminal buds of the devil's club stem are nipped and eaten, as are the root buds of the lady fern (*Athyrium cyclosorum* Rupr.). Highbush cranberry is limited in occurrence but when available, is browsed heavily. Major winter food plants are listed below:

Species	Part Utilized
Willow (*Salix* spp.)	Twigs
Elderberry (*Sambucus racemosa*)	Bark
Grasses (Gramineae)	Entire plant
Fireweed (*Epilobium angustifolium*)	Entire plant
Devil's club (*Oplopanax horridus*)	Terminal bud
Lady fern (*Athyrium cyclosorum*)	Root bud
Highbush Cranberry (*Viburnum edule*)	Twigs
Wild rose (*Rosa nutkana*)	Twigs
Blueberry (*Vaccinium ovalifolium*)	Twigs
Salmonberry (*Rubus spectabilis*)	Twigs

Range checks indicate that the utilization of willow and elderberry appears to be the best criterion for determining winter range conditions.

WEIGHTS

During the course of the open hunting seasons of 1956, 1957 and 1958, field-dressed weights of 16 male elk were obtained; in addition, both total and field-dressed weights were secured for 9 individual elk. Field-dressed weights included everything except the viscera.

Nearly all weights were taken in the field and the carcass weighed in sections. Four were taken out of the field whole and weighed on platform scales. Visceral weights were obtained by weighing the viscera and estimating the blood loss at 2½ percent of the total weight.

All weights were secured between September 1 and September 15, except for one spike bull taken on October 23. This is just prior to the active rut and males are in peak condition. All had heavy layers of fat.

Percentages of visceral weights were much lower than those recorded on Rocky

TABLE 2.—FIELD-DRESSED WEIGHTS OF 25 MALE ROOSEVELT ELK

Age Class (years)	Weight in Pounds		Number
	Average	Range	
1	455	411–495	4
2	662	606–723	8
3	780	735–842	3
4 plus	839	841–1094	10

Mountain elk (Quimby and Johnson, 1951). This may be due to various factors. All weights were obtained from male animals at the beginning of the rut. Bulls often do not feed extensively during the rut, and stomachs are not as full as they might be during other periods of the year; thus the difference between visceral and total weights of either sex is probably greater than at any other time of the year.

The visceral weights of the two yearling bulls were the only deviations. These might be attributed to the fact that these animals were not actively rutting. Three adult bulls field-dressed over 1,000 pounds, but unfortunately total weights were not obtained from any of these. It would be safe to assume, however, that the largest of the three might have weighed close to 1,300 pounds live weight.

Ages were determined by examination of the lower jaw and application of the key used for aging rocky mountain elk (Hancock and Low, 1956). No attempt was made to age elk beyond the fourth year and animals were all lumped into one age group (Table 4).

TABLE 3.—TOTAL FIELD-DRESSED AND VISCERAL WEIGHTS OF NINE MALE ROOSEVELT ELK

Age Class (years)	Weight in Pounds			Viscera Wt./ Body Wt. (percent)
	Total	Field-dressed	Viscera	
1	550	411	139	25
1	646	495	151	23
2	812	684	128	16
2	871	705	166	19
3	931	763	168	18
4 plus	1074	899	175	16
4	1054	879	175	17
4 plus	1056	893	163	16
4 plus	1155	955	200	18

TABLE 4.—ELK HUNTING SEASONS AND HARVESTS ON AFOGNAK ISLAND, 1950–1958

Year	Hunting Season Dates	Kill	Number of Hunters	Percent Successful
1950	Oct. 1–15	27	50 (permits)	54.0
1952	Oct. 1–15	15	35 (permits)	43.0
1953	Nov. 1–15	19	40 (permits)	47.0
1955	Sept. 1–15	26	105	25.0
1956	Sept. 1–20	40	135	30.0
1957	Sept. 1–20	70	250	28.0
1958	Sept. 5–15, Oct. 20–Nov. 5	111	345	32.0

ANTLERS

Antlers of mature Afognak bulls have the typical blocky appearance of the Roosevelt elk. Average measurements of 12 of the larger bulls taken are recorded in Table 5.

During the first permit hunts in 1950, 1952 and 1953, a large number of bulls taken had broken antlers. This is still common but not as prevalent as during the early hunts. Broken antlers are usually caused by sparring and fighting and a reduction in the bull population has also reduced the percentage of broken antlers during the past few years. Antler breakage may also be related to a possible mineral deficiency.

PREDATION

The Kodiak bear is the only animal on Afognak Island capable of preying on elk. In portions of the elk range bear are quite numerous, but very little evidence of pre-

TABLE 5.—ANTLER MEASUREMENTS (INCHES) OF 14 ADULT BULLS

Number of Points Left–Right	Circumference above Burr of Right Antler	Greatest Spread	Length of Longest Main Beam
7+7	14	50	48
5+5	14	49	44
5+5	12	47½	50
5+5	14	43	42
6+6	11½	34½	38
7+6	12½	46	49
5+5	10	39½	47
6+6	13	48	46
7+6	11½	38½	35½
5+5	11	43	43
7+6	11	38	47½
7+6	12	39	47

dation by bear has been found. It is very probable that a few calves may be taken during the early summer months, but the loss is not believed significant. The phenomenal population increase of the elk herd inhabiting the same range as the bear would indicate that bear predation is a minor factor.

HUNTER HARVEST

Alaska Game Regulations prohibited the taking of elk prior to 1950, although poaching by local natives was reported to have been quite prevalent before this date. In 1950, 1952 and 1953 special permit hunts were conducted, and since 1955 general open hunting seasons of various lengths have been held (Table 4).

Only bulls with forked antlers were legal prior to 1958. In the 1958 season, spikes were included in the legal take. Hunting pressure has increased each year and a total of 308 has been harvested to date.

Lower jaws were collected from a representative portion of the harvest during the past three years and classified into age groups. These are given in Table 6.

During the 1957 season a number of yearlings were taken, even though spikes were not legal. Examination of several carcasses revealed that yearlings often develop small forks. With spikes legal in 1958, the take of the yearling class increased. Many hunters at Kodiak are meat hunters and selective hunting of the smaller animals is quite common. However, because of overall heavy hunting pressure the take of the older age classes has dropped significantly, a fact which indicates that the adult bull population is being depleted. This was also apparent in post-seasonal surveys when few bulls were observed.

TABLE 6.—AGE DISTRIBUTION OF ELK KILLS, 1956–1958

Age Class (years)	Year					
	1956		1957		1958	
	No.	Percent	No.	Percent	No.	Percent
1	1	3.4	10	27.0	19	43.2
2	8	27.6	4	10.8	10	22.7
3	4	14.0	7	19.0	7	16.0
4 plus	16	55.0	16	43.2	8	18.1
Totals	29	100.0	37	100.0	44	100.0

Good distribution of the hunting is a major management problem. In 1958 the herd on Raspberry Island, which consisted of nearly 175 animals prior to the season, withstood a bull take of 46 animals, while only 10 were taken on Tonki Cape. Tonki Cape is difficult to hunt because of its exposure to heavy seas and storms. Ranges are somewhat over-utilized in this area and a planned "either-sex" season should alleviate some of this problem.

SUMMARY

Five female and three male Roosevelt elk, introduced on Afognak Island, Alaska, in 1929, have increased to 800 animals. Habitat consists of a climax spruce forest, open grassy meadows, and stands of alder, willow and elderberry.

The elk remain in large herds of 100–140 animals during most of the year and fail to break up into small harems during the rutting season. The rut is at its peak during the last two weeks of September, with calves born in late May and early June.

Food preferences are elderberry, fireweed and various grasses during the summer. During the winter, willow and elderberry are the important browse species. Devil's club terminal buds and fern root buds are also taken.

Field-dressed weights ranged from 411 pounds in yearlings to as much as 1,094 in adult bulls. Viscera comprised from 16 to 25 percent of the total weight.

Permit hunts were held in 1950, 1952 and 1953, and general open hunting seasons have been held since 1955. The annual kill has increased from 26 to 111. A total of 308 bulls has been harvested.

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AN EVALUATION OF GALLINACEOUS GUZZLERS FOR QUAIL IN NEW MEXICO[1]

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It is commonly observed that western quail often drink water, and that they are frequently found near water. Many people, perhaps partly in analogy to the human situation, therefore assume that quail cannot thrive, or even exist, in the absence of free water. Some eminent naturalists, e.g., Grinnell (1927), are among the proponents of this view. This real or supposed need of quail populations for surface water has served as the basis for extensive water development projects in several western states, including New Mexico. Very favorable management results have been reported for some of these projects (e.g., Glading, 1947; Gullion, 1954; Wright and Webb, 1957).

Not all biologists, however, agree that free water is necessary for successful maintenance of healthy quail populations, or that the provision of water in otherwise favorable areas will necessarily benefit quail. In fact, some flatly deny the importance of free water. Among the first of these was Vorhies (1928), who was convinced on the basis of his extensive field experience in southern Arizona that quail of all ages normally satisfy their water needs with plant and insect succulence and do not require surface water at all. Gorsuch (1934), in a life history study of Gambel's quail (*Lophortyx gambelii*) in Arizona, reached the same conclusion. More recently, Lowe (1955) cited further evidence supporting this idea for the same species. Much earlier, Russell (1932), as a result of a life history study he made in New Mexico, concluded that populations of scaled quail (*Callipepla squamata*) do not require drinking water. Wallmo (1956), in a life history study of scaled quail in West Texas, was unable to adduce positive proof that this species is really dependent on surface water.

Practically-motivated water-development projects for quail have gone ahead despite disagreement among biologists concerning the necessity or even the beneficial results of the water. Between 1950 and 1955, 181 gallinaceous guzzlers were installed in New Mexico, very widely distributed over the central and southern parts of the state. These guzzlers are located in various types of actual quail habitat, some good, some average, some poor. Evaluation of management results and economic feasibility is of course an important part of such a project, and this was done in New Mexico. Some evaluation was carried on concurrently with the construction work almost from its inception, but in 1953 a full-time study was begun. This was continued for three and one-half years. The results of the study are summarized in this paper.

METHODS

Use of the guzzlers by quail was the main

[1] This paper is a contribution from Pittman-Robertson Project NM-W-70-R. I wish to acknowledge the valuable field assistance rendered by R. K. Dunlap and other personnel of the guzzler construction and maintenance projects.

criterion of management value in this study, as it has been in virtually all previous guzzler evaluations. The crucial question, however, was not simply whether quail utilized the guzzlers, but whether enough birds used them to justify the high costs of construction and maintenance. The basic assumption was that the importance of water catchments is approximately indicated by the number of quail regularly utilizing the water during some critical season or seasons of the year. Although the guzzlers were studied at all seasons, it was expected that summer would probably be the most critical time. It seemed reasonable that the greatest effect (if any) of guzzlers on a quail population would be exerted through their influence on breeding birds or on young quail during the first few weeks of life.

Most guzzlers in the state were checked once a month or oftener; these included units in all areas and habitats represented. Quail use of the units was estimated in various ways. Often birds could be seen and counted, either by searching for them or by observing them as they came to the guzzlers to drink. The latter method was used especially at a number of special study units where periodic standardized morning watches were made. These watches began 30 minutes before official sunrise and continued for 5 hours, since experience showed that to be the time when most quail utilization of guzzlers occurred. Birds were tallied as they came to the guzzlers and their behavior noted. Quail of all ages paid little or no attention to a person seated in a parked car, and were thus easily observed.

Usually, however, it was necessary to estimate the number of quail which had visited a guzzler by reading sign, mainly tracks, other soil disturbance, droppings, and feathers. After several months of preliminary experience in correlating sign at guzzlers with the actual numbers of birds observed to leave the sign, we were usually able to make fairly consistent estimates from sign alone. This method might break down under high concentrations of birds, except to indicate that the concentration was high, but with our comparatively low level of quail utilization it worked well enough to be useful. The main danger of error in this method is that one is more apt to overestimate than underestimate the number of quail which have used a unit. Sometimes only two or three quail leave a surprising number of tracks.

Each time a unit was visited, all pertinent observations on guzzler operation and wildlife use were immediately recorded in a field notebook. The information routinely recorded always included what we called a use-index. These were numbers intended to express an estimate of the total quail using a guzzler. They were based on the following scale: 0 = no evidence of use; 1 = 1–10 birds (light use); 2 = 11–40 birds (moderate); 3 = 41–100 birds (heavy); 4 = 101 birds or more (very heavy). Of course, in borderline cases it was sometimes a toss-up whether to record, say, a 2 or a 3. If there was an observer bias in assigning use-indices, it was undoubtedly in the direction of larger numbers, because the observers were personally involved in the development aspects of the work. Hence, they may be presumed to have had at least an unconscious desire for the guzzlers to make a good showing. This was definitely my attitude.

The standards of guzzler use here outlined seemed to fit New Mexico conditions well, but in Nevada, for example, our "moderate" class would have been called incidental or light, and our "very heavy" (if it did not imply over 150 birds) would have been called only moderate (Gullion, 1954).

The main advantage of the use-indices was that average overall use and average maximum use of any unit or group of units over any observation period could be approximated by computing the mean of the indices recorded at successive visits. For this purpose an extended form of the use-index system, using decimal fractions, was devised. This was as follows: 0 = no evidence of use; 0.1–0.5 = avg. 5 birds (very light use); 0.6–1.5 = avg. 15 birds (light); 1.6–2.5 = avg. 30 birds (moderate); 2.6–3.5 = avg. 60 birds (heavy); 3.6–4.0 = avg. 120

TABLE 1.—AVERAGE USE OF GUZZLERS BY SCALED AND GAMBEL'S QUAIL IN NEW MEXICO DURING THREE YEARS

	1954	1955	1956	3-Yr. Avg.
Percent of total guzzlers known to be used by quail	57.8	65.5	72.2	65.8
Average use-indices (all guzzlers)	0.9	1.1	1.3	1.1
Average use-indices (positive guzzlers only)	1.6	1.7	1.8	1.7
Average of highest single use-indices recorded during each year (positive guzzlers only)	1.9	2.1	2.3	2.1
Approximate average maximum number of quail per guzzler (positive guzzlers only)	Not over 30	Not over 30	Not over 30	Not over 30

"Positive guzzlers" do not include those with zero utilization.

birds (very heavy). In our experience, the last-named class was seldom needed.

RESULTS AND DISCUSSION

Physical Operation of Guzzlers

Of the 181 guzzlers, 111 are of reinforced concrete construction and the other 70 are made of prefabricated laminated plastic. The former hold about 700 gallons of water and the latter about 650 gallons. Although New Mexico was in the grip of a severe drought during the period covered by this study (average precipitation was less than 70 percent of normal), both the concrete and plastic guzzlers proved very efficient as self-sustaining sources of permanent water. Only a few "leakers" ever went dry, and these were repaired. Precipitation in guzzler areas during the period studied averaged only about 7 or 8 inches per year. Yet, on the basis of 3,568 separate observations, the concrete guzzlers maintained yearlong water at an average 68 percent of capacity, and their average annual minimum was 52 percent. On the basis of 1,122 observations, the plastic guzzlers maintained yearlong water at an average 89 percent of capacity, with an average annual minimum of 76 percent. These results were secured with water-collecting surfaces of about 270 square feet per guzzler for both types of unit. Water levels were generally highest during the hottest parts of the year, since under the New Mexico rainfall pattern most replenishment occurs in summer. Despite very limited flushing action when guzzlers sometimes ran over, stored water seldom became objectionably foul, as so often happens with small bodies of standing water exposed to direct sunlight. Water temperatures were moderate. The annual average was about 55°F., with average maxima and minima of about 70° and 40°. Water temperatures of course varied somewhat with latitude and altitude, but the temperature spread was not great between northern and southern guzzlers or those at different elevations. Guzzlers were located between about 32° and 36° north latitude. Elevations above sea level varied from about 3,000 to 6,500 feet. Nearly all guzzlers were oriented so as to open toward the north or east, but exceptions showed that other directional facings did not result in significant differences in physical performance or game use.

Biological Findings

The following data are based on 3,772 guzzler checks made during the three-year period 1954–56. It was not possible to separate scaled and Gambel's quail in the tabulations because a number of units were regularly used by both. For evaluation purposes, this is probably immaterial since the reaction of the two species to the guzzlers was not noticeably different.

Tables 1 and 2 summarize guzzler utilization. Both tables are mainly self-explanatory. "Positive guzzlers" were those definitely known to be used by quail, i.e., this omits those with zero utilization. A gradual increase in the percentage of total guzzlers used by quail, and in the degree of utiliza-

TABLE 2.—PROPORTIONS OF TOTAL GUZZLERS SHOWING VARIOUS HIGHEST RECORDED USE-INDICES FOR SCALED AND GAMBEL'S QUAIL IN NEW MEXICO DURING THREE YEARS

Highest Recorded Use-index	1954		1955		1956	
	Number	Percent	Number	Percent	Number	Percent
0	27	18.7	24	13.3	20	11.0
1	33	22.8	38	21.0	31	17.1
2	61	42.1	75	41.4	68	37.6
3	23	15.7	41	22.6	49	27.1
4	1	0.7	3	1.7	13	7.2
Totals	145	100.0	181	100.0	181	100.0

tion is seen in Tables 1 and 2. The latter presents a breakdown by proportions of total units showing the various highest recorded degrees of quail use during each of the three years. A progressive increase in the proportions of guzzlers exhibiting higher use-indices is seen in the table. The reason for these apparent increases is not known. Strictly comparable information for subsequent years is not available, but general observations have given no hint that the trend toward greater use shown in these tables has continued to a significant extent in the years since 1956.

A total of 48 game watches, including all seasons, were made at 8 guzzlers. These were standardized watches, 5 hours long, beginning one-half hour before official sunrise. The maximum numbers of quail ever observed to come to the 8 guzzlers were as follows: 0–17–19–20–28–34–40–41 (average of maxima, 24.9). More quail were known to use certain other guzzlers at times, but as a series these eight were probably about average.

Table 3 shows seasonal quail use of the guzzlers. It is apparent that, although the number of units used by at least a few quail was about the same in spring, summer, and fall, the greatest concentrations of quail definitely tended to occur in the fall when the birds were near their annual peak of abundance. Heavy use in summer was exceptional. This is the reverse of the situation reported from California, Nevada, and Arizona. There the greatest concentrations are reported to occur around guzzlers and other isolated water sources in summer, i.e., the breeding and rearing season. Summer concentrations of 300 or more quail per guzzler are apparently common, at least in California and Nevada, while 600 or more are

TABLE 3.—SEASONAL DISTRIBUTION OF GUZZLER USE BY SCALED AND GAMBEL'S QUAIL IN NEW MEXICO (POOLED DATA, 1954–56)

Season	Total Evaluation Checks	Use-index									
		0		+ (1,2,3,4)		3		4		3+4	
		No.	Percent	No.	Percent	No.	Percent	No.	Percent	No.	Percent
Winter (Jan.–Feb.–Mar.)	937	391	41.7	546	58.3	76	8.1	3	0.3	79	8.4
Spring (Apr.–May–Jun.)	1,166	313	26.8	853	73.2	22	1.9	0	0	22	1.9
Summer (Jul.–Aug.–Sep.)	887	288	32.5	599	67.5	57	6.4	2	0.2	59	6.6
Fall (Oct.–Nov.–Dec.)	782	218	27.9	564	72.1	106	13.6	14	1.8	120	15.4
Totals	3,772	1,210	32.1	2,562	67.9	261	6.9	19	0.5	280	7.4

Percents are proportions of the guzzler checks made during each period.

said to be not at all unusual. In New Mexico, on the other hand, summer use of a guzzler by 30 or 40 quail would be unusually high. This difference may go far toward explaining the poor showing of guzzlers in New Mexico compared to those farther west. It seems reasonable to assume that guzzlers could increase quail numbers, if at all, chiefly by exerting a beneficial influence on breeding or on survival of young. That this does not seem to have occurred to a significant degree in New Mexico suggests that guzzlers there are probably ineffective in quail management.

Climatic contrasts between the two areas probably account for the observed differences. Like the other states named, New Mexico is arid to semiarid, but the seasonal distribution of precipitation is distinctly different (U.S. Dept. Agric., 1941). This is probably the critical factor governing the reaction of quail to guzzlers. Normal average annual precipitation in the parts of New Mexico where scaled and Gambel's quail occur varies from about 8 to about 15 inches. Most of this falls as rain. Between two-thirds and three-fourths of the annual total is received from April through September. During July and August, the months of greatest rainfall, nearly one-third of the annual total is normally received. The greatest number of days with precipitation also occur during July and August. The climate of New Mexico may therefore be characterized as one of summer rains and winter drought. Thus, at the very time when the annual crop of young quail is being produced, the normal rainfall pattern in New Mexico favors wide dispersal of the birds, to take full advantage of green succulence and insects, rather than concentration around permanent water. On the other hand, the normal rainfall pattern in guzzler areas of California and Nevada is one of summer drought and winter rains—exactly the reverse of the New Mexico pattern. In the former areas, nearly all the annual rainfall occurs in winter and summers are normally very hot and dry. The situation in Arizona is somewhat intermediate. The pattern in western Arizona is more like that in California and Nevada, while central and eastern Arizona approach the New Mexico type of climate. Actually, in much of Arizona there are two wet seasons, a maximum in the July–September period and a smaller peak from December through March. It may be significant that the reported success of quail guzzlers in Arizona also seems to have been somewhat intermediate.

Concerning the probable influence of climate on the need for free water, it is interesting that on Tiburon Island in the Gulf of California where Lowe (1955) reported a thriving population of Gambel's quail in the virtually complete absence of surface water, the rainfall pattern is very similar to that in New Mexico.

No really objective standard of guzzler performance is possible, but for the sake of discussion consider this: to me it seems reasonable to believe that a guzzler, to justify its cost (see next section), should make available at least 4,500 harvestable quail during an expected guzzler life of 30 years. This would be at the rate of 150 quail per year—10 limits of 15 birds, for example. These must be quail which are needed and utilized, and which would not otherwise be available. The word "harvestable" must be emphasized, for to produce a hunting surplus of 150 quail annually a total fall population of at least 375 would probably be required. This assumes a 40 percent kill, and even this is difficult to achieve. It is obvious how far short of such a standard, or of one even half as rigorous, the New Mexico guzzlers came during the study. Fall concentrations of as many as 200 quail probably did occur rarely at a few guzzlers (this was at least partly due to a grain feeding program also practiced at all units), but average maximum (total) utilization probably did not exceed 30 quail per unit. Furthermore, most if not all of these birds would apparently have existed even without guzzlers, judging by what happened in areas of the state where there were no guzzlers.

Economic Considerations

At current prices, guzzlers are expensive items. When all applicable charges are in-

cluded, those in New Mexico cost, on the average, over $1,000 apiece to build. This included a stock-tight fence enclosing from 1 to 2 acres around each guzzler. Even with fences only large enough to keep livestock off the actual structures, additional guzzlers today probably would cost at least $1,000 each, in view of the continued rise in prices and wages since 1955.

Actual and potential quail range in New Mexico probably covers at least 50,000 square miles. Obviously, the 181 guzzlers we built (at a cost of over $200,000) are a mere drop in an extremely large bucket, considering the vast extent of quail range and the very limited mobility of quail. Allowing a liberal 4 square miles over which a given guzzler might conceivably influence quail, the number of units required adequately to service even half of the state's total quail habitat runs into several thousands, and the construction and maintenance costs into astronomical figures.

CONCLUSIONS

This study confirmed the fact that guzzlers offer an efficient means of providing permanent water in dry regions even during unfavorable climatic periods.

Nevertheless, the biological findings cast grave doubt on the actual value of guzzlers, hence of any similar development of surface water, in the practical management of quail under a climatic pattern of summer rains and winter drought such as exists in New Mexico and in many other parts of the West. Quail utilization of the guzzlers studied was by no means great enough to justify the high costs of construction and maintenance. Possible future changes in quail response could conceivably modify this conclusion, but barring important changes it is my considered judgment that guzzlers are not sufficiently effective to be practical in New Mexico quail management on a publicly financed basis. The possible role of guzzlers in privately financed shooting preserves is beyond the scope of this discussion.

SUMMARY

Between 1950 and 1955, the New Mexico Department of Game and Fish built 181 gallinaceous guzzlers, primarily for scaled quail. The overall cost exceeded $1,000 per unit. The results were evaluated mainly during the 3-year period 1954–56. Use of the guzzlers by quail was the main criterion of management value. Average total quail use probably did not exceed 30 birds per unit per year. Only about 7 percent of the 181 guzzlers ever reached quail utilization levels of over 100 birds at any time during the study. At a few guzzlers, fall concentrations of as many as 200 quail probably sometimes occurred, but this was rare. Considering the low levels of utilization ordinarily found, and the high costs of construction and maintenance, it was concluded that guzzlers are ineffective and impractical for quail management in New Mexico. Judged solely on their efficiency as devices for providing permanent water, the guzzlers were, however, amazingly effective.

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CENSUS OF PLAINS ANIMALS IN THE SERENGETI NATIONAL PARK, TANGANYIKA

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In mid-1957 the director of the National Parks of Tanganyika, British East Africa, Colonel Peter Molloy, approached us with a request to count the number of large animals in the Serengeti National Park and to establish the extent of their seasonal movements. The Serengeti Park, the only national park in Tanganyika, was created to protect the last great plains animal herds and their habitats throughout their life cycles.

In Northwest Tanganyika there are still large concentrations of plains animals, particularly the wildebeest (gnu), zebra, and Thomson's and Grant's gazelles. Presumably, they are the last herds of great magnitude still existing in Africa. Their total numbers were generally considered to be above one million. The government was planning to reduce the size of this national park and change the boundaries on behalf of the Masai natives, chiefly in accordance with the recommendations laid down in the Pearsall report (1957). With regard to the movements of the large herds, however, Pearsall's otherwise thorough study is necessarily based mainly on assumptions of others and short observations of his own. Therefore, it appeared essential to establish first the number of animals living there, and whether the animal herds actually were protected by the present boundaries and proposed new boundaries. As far as we know, aerial censuses of the whole visible animal population have not been carried out. Up to now, aerial censuses apparently have been restricted to one or two species. The first prerequisite appeared to be to assess the number of the dominant characteristic animals. This work is reported here.

[1] Michael Grzimek died in an air accident at the end of these investigations. An obituary appeared in The Journal of Wildlife Management, 23(3): 368–369, July, 1959.

We wish to express our sincere thanks to Dr. Georg Borgstrom for the translation and to Dr. George A. Petrides for his help in editing this publication.

Methods

The large size of the area, 4,600 square miles, ruled out the idea of observing and counting the animal herds on the ground. This would have not been feasible for technical and economic reasons. As the plains region and also a major part of the mountainous area are completely devoid of trees, conditions were ideal for counting animals from the air and consequently this was the method used.

The flights were made by a special German Dornier aircraft, DO-27, which permitted a minimum velocity of 30 m.p.h. with a consequent ability to land on very short strips and on rough ground. The plane was painted in conspicuous stripes (Fig. 1) to facilitate detection in case of emergency landing. The cabin allowed excellent visibility in all directions. There were no wing struts to reduce visibility.

At first, the intention was to fly over the whole area in strips and to photograph it entirely with automatic cameras. It turned out, however, that in order to distinguish reliably between different animal species, low altitude photographing (approximately 2,400 feet) would be needed. At this altitude, however, over 50,000 vertical exposures would have been required to cover the entire area. For economic reasons, this procedure had to be abandoned. The lack of landmarks over much of the area also made it impossible readily to put together oblique individual photographs from adjacent areas. It would be very difficult afterwards to establish on the pictures where one parallel strip started and where another one ended.

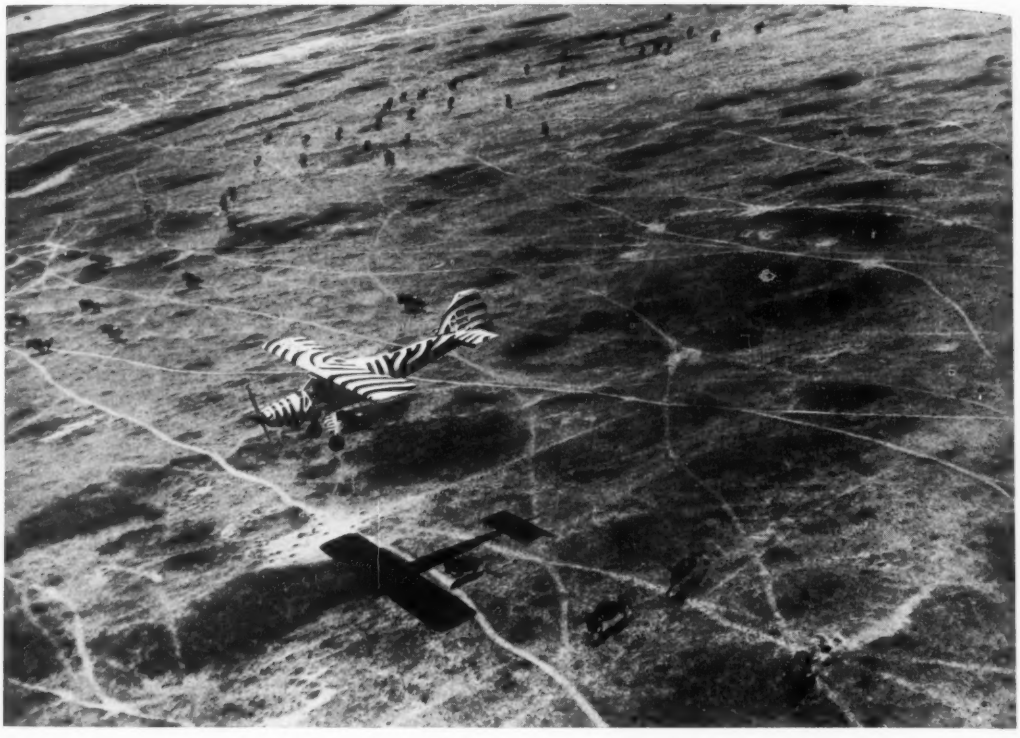


FIG. 1. The Dornier 27, used by the authors for the game census, was capable of extremely slow airspeed and landing on rough ground. The usual flying altitude was higher than shown here. Animals fled only short distances to both sides and remained in the counting strip. The lines on the ground are trails made by the animals. Wildebeests and a single zebra can be seen.

After excluding these alternatives, we decided to subdivide the area into small districts (Fig. 2) and fly through each of these along parallel belts, counting the total number of animals which could be seen under a certain angle of vision on both sides of the aircraft. Areas 5 and 28–32 immediately bordered the park limit. Only wildebeests were counted on Area 31 and in Area 32 only wildebeests and zebras. Other antelopes appeared here only in small numbers.

In mapping out major areas, natural boundaries such as river valleys and mountain ranges were taken into consideration so that animals could not readily move from counted areas into areas not yet flown.

After several test flights the width of strip was fixed at 550 yards on either side of the aircraft. This required a flying altitude of 150–300 feet. At 1,500 feet an observer could readily distinguish between antelope species and classify them as adults or young. For economic reasons, however, the width of the strips was extended to 2,000 feet on each side in areas which were particularly easy to scan and poor in number of animals. In the eastern mountainous regious, only the crater bottoms and broad valleys with open pastures were well covered by flights (Fig. 2, Areas 1–10). In areas with tropical rainforests, as at the southern and eastern limits of the Ngorongoro Crater, counting was impossible due to lack of visibility and efforts were abandoned there.

The left-hand observer was aided by a strip of plastic on the window, which indicated the approximate limits of his angle of vision. On the right front window this method could not be applied, however, due to curvature of the windowpane. Of the total number of animals counted (see below), 51.3 percent of the animals were seen

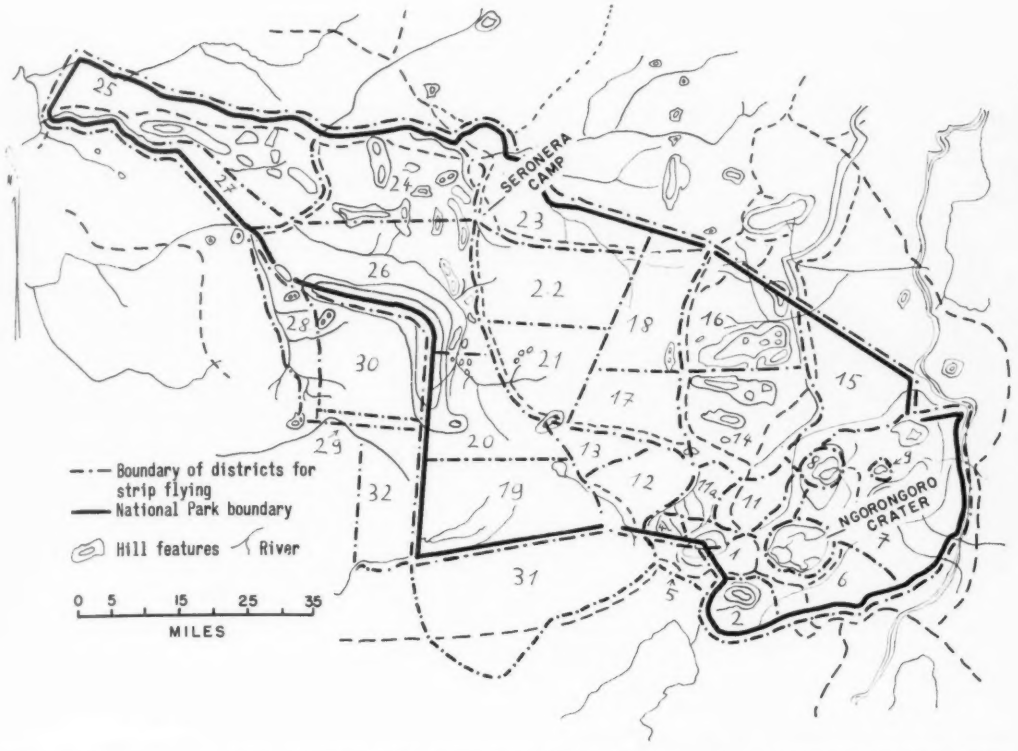


FIG. 2. The Serengeti Area, showing Park boundaries in 1958 and numbered districts for strip flying.

on the left-hand side and 48.7 on the right-hand side. This suggests that errors on counting due to the location of the observers in the plane probably were not serious.

Prior to the first counting and whenever introducing new persons to the census operations, we made these individuals acquainted with the observation angle and width of strips through flying over test strips delimited by limed stones. As these strips were frequently passed when taking off and landing, the counter always had the opportunity to refresh his memory as to the width of an observation strip.

The task of the pilot was to navigate and in each case to establish the width of the strips and their mutual order. As no maps were available, the park area had to be flown over on the basis of very incomplete sketches in which only large streams, rivers, parts of the mountains, and some pastures were indicated. The pilot also had to orient himself on the basis of such landmarks as solitary trees, rock outcrops, water holes, and groups of bushes. He flew according to an accurate compass course almost exclusively in an east-west direction or the reverse. As a very strong easterly wind blew constantly during the entire period, the aircraft flying in this way was least drifted off course. When flying above a strip, the pilot observed certain landmarks which constituted its lateral limitation. In turning around and starting to fly the next adjacent strip, these marks constituted the new extreme limitation to one side. The senior author served as pilot during all counting operations in order to maintain continuity.

One area, outside the park, where the herds of the wildebeests could be readily counted, we flew at an altitude of 2,000 feet and covered strips 4,500 feet on each side. This, however, was feasible only because the land was completely flat with no trees whatsoever. Ninety percent of the animals there consisted of wildebeests which were orien-

tated in long lines. At this altitude and with this width of strip, zebras and wildebeests could easily be distinguished from each other. Gazelles could be identified only with difficulty however, and distinguishing between different species of antelopes, e.g., topi and kongoni, was no longer possible.

At the end of a strip the plane always was turned at a higher altitude in order to better establish the exact position of the new strip. The length of the strips was different depending on the size and position of the district which was flown over. The greatest length was about 37 miles. The park warden for each area assisted in the counting. We were also assisted on the eastern part by Mr. Gordon Harvey and for the western part by Mr. Myles Turner, and the Director of National Parks, Col. Peter Molloy. The junior author counted during the entire period.

When the landscape could be readily scanned and the number of animals was sparse, we flew at 140 m.p.h. As the pilot had very good visibility, he could on short notice reduce velocity to 30 m.p.h. Through such adjustments, counting was very much facilitated. Slow airspeeds were also maintained when animals were dense and where acacias and other trees were very sparsely distributed. There it was imperative to fly at low speed in order to identify and count animals under the tree canopies.

Counting flights were made mostly in early mornings and late afternoon when it was cool and pleasant. We were not compelled to take into consideration any special daily rhythms of the animals. Large zebra and antelope herds were never seen to withdraw during the heat of the day. Even quite late in the morning one could see hyenas, jackals, and vultures consuming animal remains from the previous night. In the afternoon, however, most of these disappeared.

In a few areas the pilot assisted the observers by taking over the task of counting one or two rare animal species on both sides of the plane. All counters jotted down the numbers of counted animals as they were censused. For control purposes, two counters often counted the animals on the same side and compared their results later. Counters could communicate with each other and and with the pilot during the flight through an intercom system. After landing, the figures were summarized.

ANIMAL REACTIONS TO THE AIRCRAFT

Reactions of the animals to the airplane were different, depending on numerous factors. Solitary animals reacted only slightly to the aircraft flying above, even at an altitude of only 30–60 feet. This was true for both gazelle species and also for zebras, kongonis, and topis. Resting Thomson's gazelles did not even stand up when the airplane flew just 60 feet over them. Small herds of 5–15 zebras or antelopes ran about 100 yards from the path of the aircraft. In this case, at the last minute the animals often dashed straight across the path of the airplane as they typically do for motorcars in the Serengeti.

Larger herds of 50 animals or more reacted differently. Wildebeests, in particular, were extremely nervous. They started racing away when the airplane flew at an altitude of even 200 yards even though animals standing alone showed no reaction at all. When in herds they also dashed off more persistently, stopping only several hundred yards away. A few particularly nervous animals seemed to initiate escape reactions within the herd and the others followed suit.

Thomson's and Grant's gazelles in large concentrations showed quite another type of flight reaction. The herd remained calmly at its original place and at the very last minute, when the aircraft was straight above, they ran in all directions in a confused way, but only for a few seconds until the plane had passed.

Zebras noticed the airplane even when it was coming in for a landing with the motor shut off and at an altitude of 150 feet. Ostriches ran only when the aircraft was quite close. Otherwise, they exhibited the typical threat posture with inflated feathers and spread wings. Giraffes were quite difficult to start moving. They fled only rarely and then only approximately 150 feet to the

side. When standing under trees, they did not run at all. Baboons immediately ran to nearby trees.

Hyenas with prey (e.g., a young gazelle) always fled while the airplane was still at some distance. Specimens asleep near a water hole could not be chased away. In extreme cases they might wake up, rise and have a good look at the airplane. Sometimes the hyenas were stimulated by the flight of antelopes and ran with them for a few yards.

Wart-hogs fled promptly in their common attitude, the thin tail held straight upward. In one case a wart-hog was seen to hide in a burrow. A family of about ten foxes also headed for their burrow and disappeared when the plane approached them at a distance of 150 yards.

Lions reacted in different ways. In the Ngorongoro Crater, we flew above and circled around an adult male. At the beginning he did not react much. Finally he started to walk away, gradually walking faster. In most cases lions tried to make themselves invisible in the grass by pressing themselves close to the ground.

In those rare cases when cheetahs were sighted they remained sitting and showed no fright whatsoever. They merely watched the plane. The single leopard which we observed dashed to a tree and climbed it.

Larger birds, such as the European stork, crowned crane, and bustards made short flights 10–20 yards to the side when the aircraft flew above them at an altitude of less than 120 feet. When we flew more to the side of the birds, no movements took place or they were restricted to a short run. Bustards reacted with a horizontally protruding neck being turned around to follow the airplane with one eye upwards. In this angular position they would run away, moving laterally. Only in case of a strong disturbance by the airplane did they actually take to the air.

Vultures and other predatory birds on the ground mostly remained at their prey. Birds in flight (predators as well as storks) moved out of the way of the plane only at the last minute. Predatory birds then turned sharply to the side with their spread wings held vertically. We were aware that even very small birds when hitting an aircraft sometimes cause serious disasters, so we kept away from all birds as much as possible.

When such birds as vultures and buzzard-hawks sailed in the same direction as the plane was flying, it was possible to fly past them at the same altitude if the plane's speed was low and the estimated distance at least 25 yards. The birds only looked closely at the aircraft. In the air, these birds may feel that there is nothing to endanger them, which would explain their lack of escape reaction.

Large swarms of birds the size of starlings frequently flew up when the plane was approaching. These birds kept very close to the ground, however, flying extremely low and frequently changing their direction, presumably a typical flight reaction against small or predatory birds.

Flamingos flew up when we approached them from an altitude of 7,500 feet. This was established through special test flights. In this case it did not seem to matter whether the flocks consisted of 6–10 individuals or 1,000. In any case they flew together and at right angles to the plane's path. Their unpredictable maneuvers on the wing made it impractical to approach them closer than 300 feet.

The approaching aircraft sometimes caused animals to flee into strips which already had been counted. But in most cases they did not move more than 100–200 yards and remained within the zone being counted. Where conditions permitted, we flew at altitudes sufficiently high to avoid appreciable fleeing or we resorted to the method of counting entire herds. Due to all these flight reactions, we flew to higher altitudes as soon as we spotted larger herds in order not to drive the animals into strips which were already counted. We circled around such a larger herd without disturbing it and, disregarding the strips, counted the whole herd.

SOURCES OF ERROR

Sources of error were eliminated as far as possible. In counting individual areas,

great differences were sometimes encountered between results from the two sides due to the fact that the animals were not uniformly distributed over the plains. They often concentrated in herds and frequently gathered in great numbers around waterholes.

One disturbance that presumably could never be completely obviated was the natural movement of animals from a counted strip into an uncounted one and the reverse. We tried to reduce this error to the utmost by counting in the same day areas that had no natural obstacles between them. As a whole, we constantly strove to count consecutively one area bordering another.

To avoid errors due to disturbance does not seem to be entirely possible even if the entire area were photographed. These errors became particularly large when animals were migrating at the time of the counting. In the course of our observations, we could establish no special directions for the movements of animal herds in particular areas. A widespread breakup of the herds and more intense movement of groups began about January 15 when we had almost terminated our studies.

Directly beneath the airplane was a blind angle which none could observe. Due to the fact that we were flying very low, the area involved was extremely small. In addition, most animals ran in all directions to the side and made this zone free, so that this source of error probably was not important.

Due to long distances into the study areas and back, it frequently became necessary to count for more than two and one-half hours with an obvious exhaustion both of counters and pilot. Several hours of rest were required after each trip.

Another possibility for error arose when the sun was low. We had placed the strips chiefly in the east-west direction, and fewer gazelles were always observed when flying toward the sun as compared to flying the opposite direction. Then the animals were sharply illuminated by the sun. Errors due to this cause were of a different magnitude depending on the animal species. The conspicuous giraffe and the rhinoceros, for instance, could hardly be overlooked. These animals could be spotted at an extremely distant range, and it was more likely that they would be counted twice rather than that they be missed. For the giraffe, rhinoceros, elephant, oryx, roan antelope, and probably for buffalo, the figures given in

TABLE 1.—RESULTS OF AERIAL GAME CENSUS OF THE SERENGETI AREA—JANUARY 3–16, 1958

Common Name	Scientific Name[1]	Number
Thomson's Gazelle	*Gazella thomsonii thomsonii.* Gunther, 1884.	194,654
Grant's Gazelle	*Gazella granti robertsi.* Thomas, 1903.	
Wildebeest (Gnu)	*Connochaetus taurinus albojubatus.* Thomas, 1892.	99,481
Zebra	*Equus burchellii Boehmi.* Matschie, 1892.	57,199
Topi	*Damaliscus korigum eurus.* Blaine, 1914.	5,172
Eland	*Taurotragus oryx pattersonianus.* Lydekker, 1906.	2,452
Impala	*Aepyceros melampus melampus.* Blyth, 1866.	1,717
Black Buffalo	*Syncerus caffer aequinoctialis.* Blyth, 1866.	1,813
Kongoni (Coke's Hartebeest)	*Alcelaphus buselaphus cokii.* Gunther, 1884.	1,285
Giraffe	*Giraffa cameloparadalis tippelskirchii.* Matschie, 1898.	837
Waterbuck	*Kobus defassa raineyi.* Heller, 1913.	284
Stork	*Ciconia ciconia ciconia.* Linné.	178
Oryx Antelope	*Oryx beisa callotis.* Thomas, 1892.	115
Elephant	*Loxodonta africana africana.* Blumenbach, 1797.	60
Roan Antelope	*Hippotragus equinus langheldii.* Matschie, 1898.	57
Rhinoceros	*Diceros bicornis bicornis.* Linné.	55
Ostrich	*Struthio camelus massaicus.*	1,621
Total		366,980

[1] After Allen (1939).

the table are considered to be very accurate. Elephants, rhinoceros, and buffalo occurring in rainforests, however, were not included.

Some errors could have occurred in the counts of the larger herds of wildebeests, zebras, and gazelles. Some herds of 2,000 or more were observed.

It is possible that a margin of error of approximately 20 percent in the number of counted animals could exist, but the error should not exceed that level.

RESULTS AND DISCUSSION

The total number of each species found in all areas is given in Table 1. The distribution of all animals at the beginning of January is shown on Figure 3. In Figures 4–13 the distribution of animals is presented graphically by species. Figure 14 covers several uncommon species, as indicated by distinctive symbols.

It was evident from preliminary counts that movements of several species were not limited by park boundaries. During some seasons, a great number of animals leave the park area. Figures 5, 6, 9, and 12 make this clear for wildebeests, zebras, topis, and buffalo, respectively.

In the Plains of Salei, a grass plain extending north from Area 5, the density of wild animals declined very rapidly from the boundary of the park to the north.

On the basis of our findings as regards distribution, a whole series of new questions arise. The animals of one species are not regularly distributed over the entire area but form concentrations in certain places, while in other areas they are entirely missing. As regards the giraffe, the reasons for this are clearly indicated. The animals stay among trees or in their vicinity. Waterbucks only occurred along the river sides or in parts of the Ngorongoro Crater. Impala occurred only in dense bush and tree plains areas and did not occur on the open plains. This also was true for the topi, although less strictly so. The interpretation as regards the gazelles is more complicated. We have not been able to find, so far, any explanation for the fact that they do concentrate in certain definite regions within the steppe. The same is true for the wildebeest. Possibly soil types and indirectly the composition of the vegetative cover play a role. Gazelles also could be pushed out of an area into regions with a poor vegetation through population pressure by the closely associated wildebeest. At any rate it was conspicuous how one species fits into the openings left by another one. Similar conditions prevailed for zebras, although they overlapped with wildebeests in large areas. Movements of the game populations were studied by marking individual animals and by following them by plane, and will be reported in a separate publication. We also initiated studies of soil types and vegetative cover.

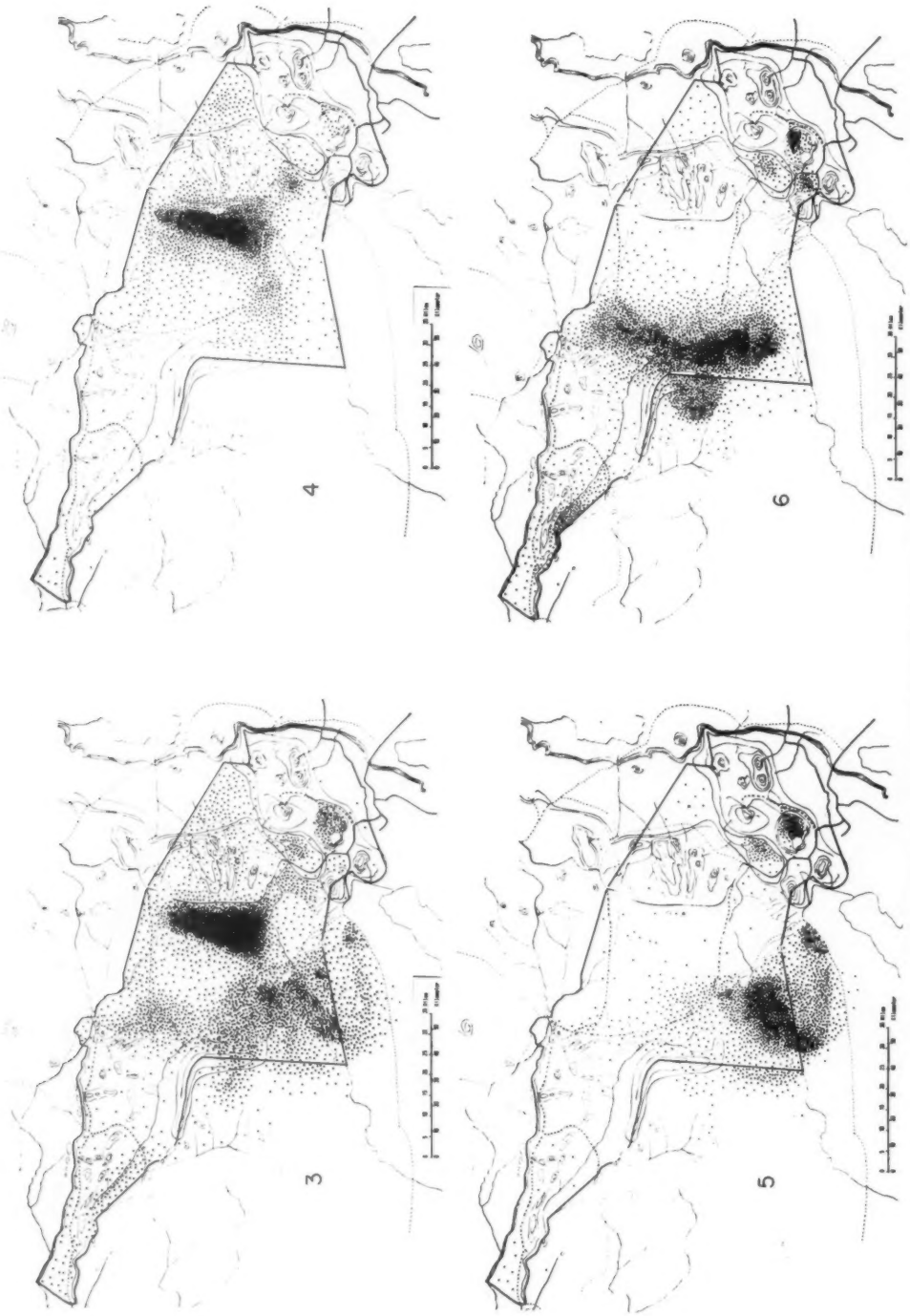
SUMMARY

The number of plains animals was studied in the Serengeti National Park in Tanganyika, British East Africa. This area of 4,600 square miles was subdivided into 32 smaller areas and the animals were counted from the air. Each area was flown in parallel strips at low altitude with a specially-built airplane. The total count of large animals was 366,980, only one-third of the number which earlier had been estimated for this region.

These animals presumably are the last large concentrations of plains animals in Africa. A considerable number of animals were found at the time of our census in the area outside of the park. A far greater number will be outside of the park on the basis of contemplated future boundaries. Studies of the seasonal movements, and their causes, of these animal herds are in progress. The reaction of different species to the aircraft are described.

ZUSAMMENFASSUNG

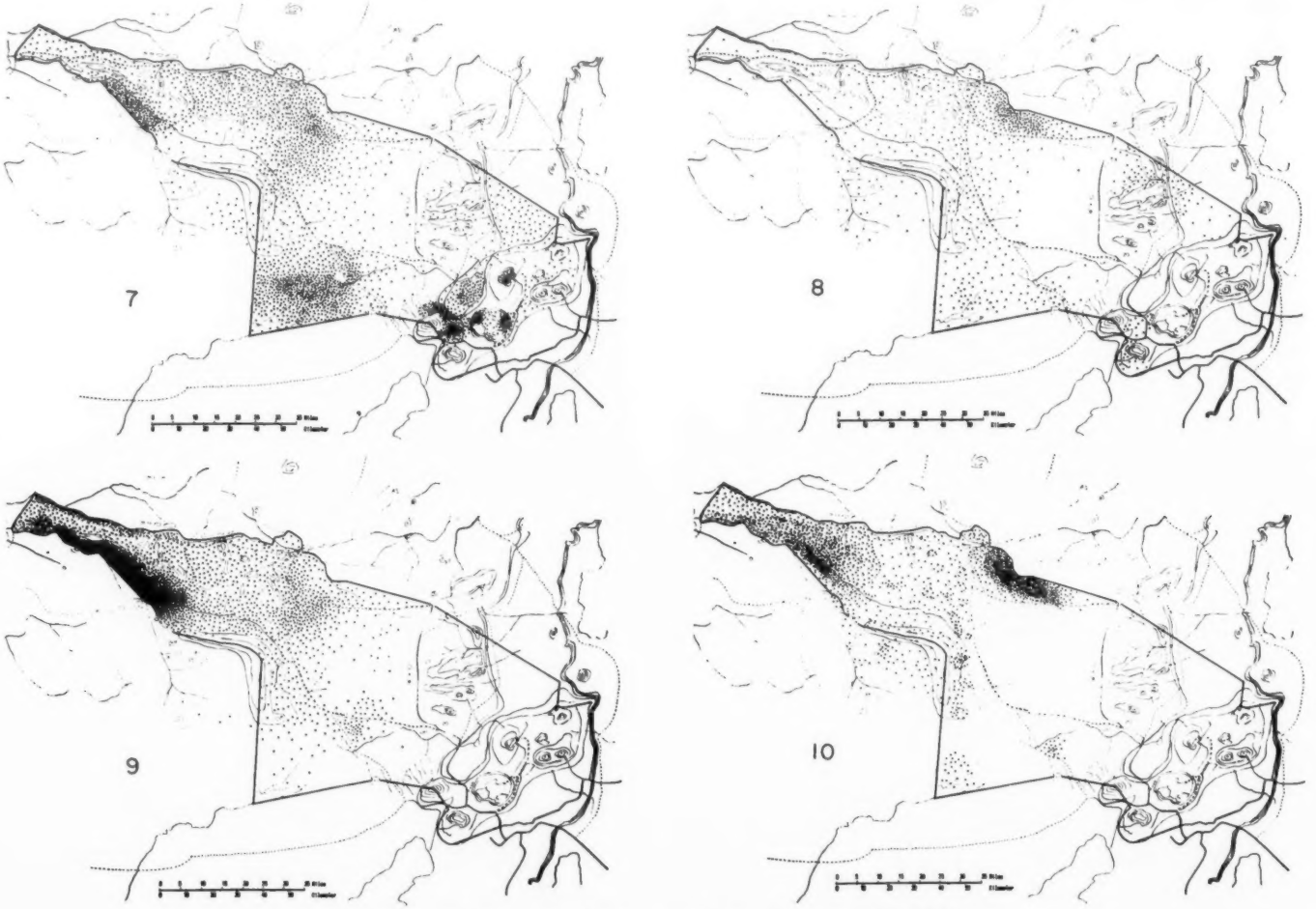
Die Zahl der Steppentiere wurde im Serengeti National Park in Tanganyika, British Ost-Afrika, untersucht. Dieses Gebiet von 12 000 qkm wurde in 32 Zählbezirke eingeteilt und die Tiere wurden von der Luft aus gezählt. Jeder Distrikt wurde in parallelen Streifen in niedriger



Aerial Game Census in the Serengeti Area, January 3–16, 1958.

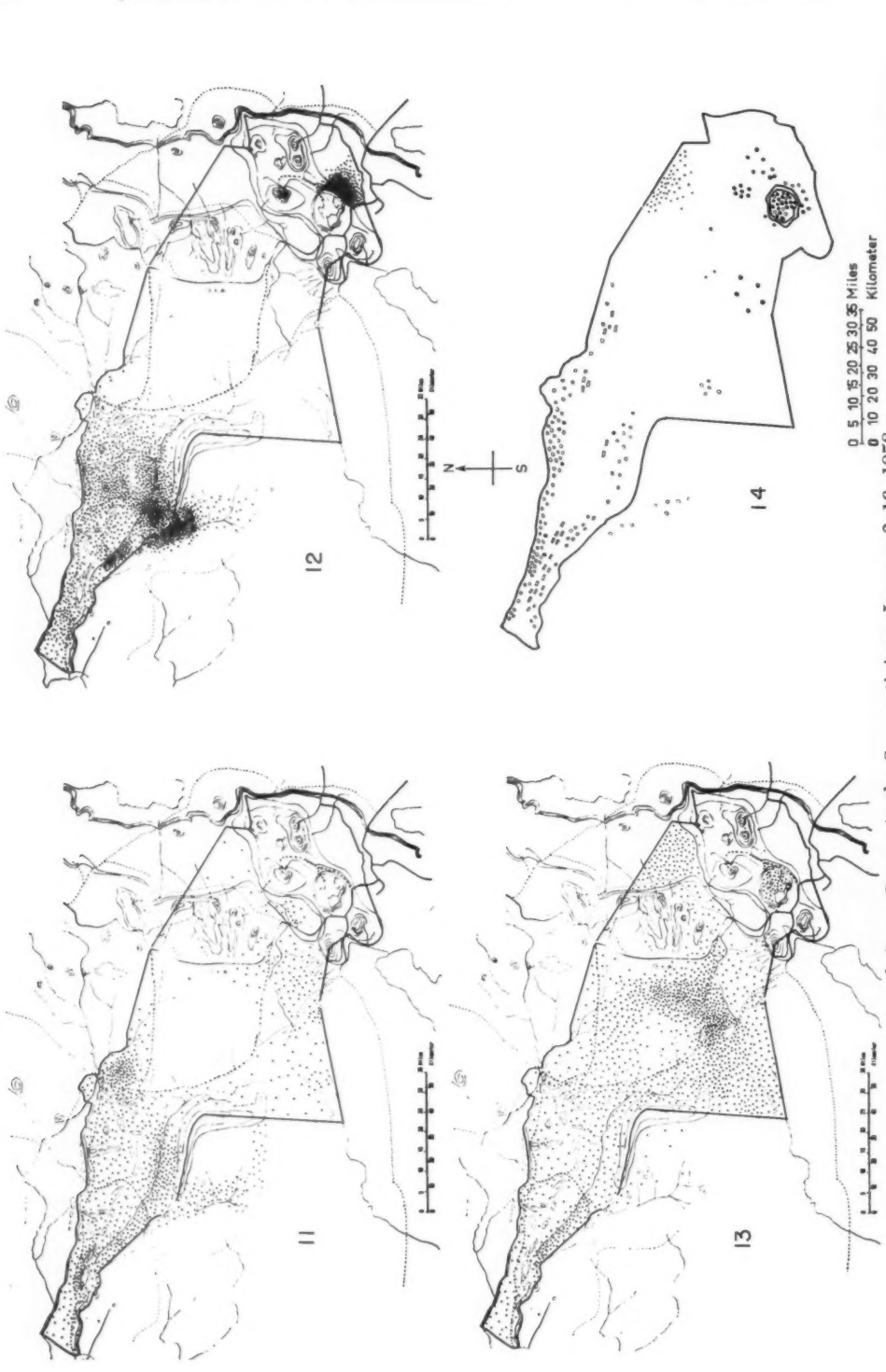
FIG. 3. Distribution of game in general. 1 point = 100 animals. FIG. 4. Distribution of Thompson's and Grant's gazelles. 1 point = 100 animals. FIG. 5. Distribution of wildebeest. 1 point = 50 animals. FIG. 6. Distribution of zebra. 1 point = 20 animals.

FIG. 3. Distribution of game in general. 1 point = 100 animals. FIG. 4. Distribution of Thompson's and Grant's gazelles. 1 point = 100 animals.
FIG. 5. Distribution of wildebeest. 1 point = 50 animals. FIG. 6. Distribution of zebra. 1 point = 20 animals.



Aerial Game Census in the Serengeti Area, January 3–16, 1958.

FIG. 7. Distribution of eland. 1 point = 1 animal. FIG. 8. Distribution of kongoni. FIG. 9. Distribution of topi. 1 point = 2 animals. FIG. 10. Distribution of impala. 1 point = 1 animal.



Aerial Game Census in the Serengeti Area, January 3–16, 1958.

FIG. 11. Distribution of giraffe. 1 point = 1 animal. FIG. 12. Distribution of buffalo. 1 point = 1 animal. FIG. 13. Distribution of ostriches. 1 point = 1 animal. FIG. 14. Distribution of miscellaneous game. Small dot = 2 oryx; large dot = 1 black rhino; open circle = 2 waterbucks; rectangle = 2 roan antelope.

Höhe mit einem dafür besonders geeigneten Flugzeug abgeflogen. Insgesamt wurden gezählt 194 654 Gazellen (Thomson- und Grant-Gazellen); 99 481 Gnus; 57 199 Zebras; 5 172 Topi-Gazellen; 2 452 Elen-Antilopen; 57 Pferde-Antilopen; 55 Nashörner; 1 717 Impala; 1 813 Kaffernbüffel; 1 285 Kongoni-Antilopen; 837 Giraffen; 284 Wasserböcke; 178 Störche; 115 Oryx-Antilopen; 60 Elefanten; 1 621 Strausse; insgesamt 366 980 grössere Tiere. Das ist nur ein Drittel von der Zahl, die früher geschäzt worden war.

Diese Tiere sind offensichtlich die letzten grossen Konzentrationen von Steppentieren in Afrika. Eine beträchtliche Menge der Tiere lebte während der Zählung in dem Gebiet ausserhalb des Parkes. Eine noch grössere Menge wird sich ausserhalb des Parkes aufhalten, wenn die beabsichtigten neuen Grenzen in Geltung treten. Untersuchungen der Wanderungen dieser Tierherden und ihre Ursachen sind im Gange, jedoch nicht Gegenstand dieser Veröffentlichung. Die Reaktion verschiedener Tierarten auf das Flugzeug wird beschrieben.

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FIG. 14. Distribution of miscellaneous game. Small dot = 2 oryx; large dot = 1 black rhino; open circle = 2 waterbucks; point = 1 animal. rectangle = 2 roan antelope.

AN EVALUATION OF THREE AGE DETERMINATION CRITERIA IN LIVE BEAVERS

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The purpose of this paper is to evaluate three criteria for determining the age of live beavers. The three criteria to be examined are weight, the product of tail dimensions, and the breadth of the skull across the zygomatic arches. A real need exists for study of nearly all beaver aging criteria, because there is much disagreement in the existing literature concerning methods of beaver age determination. This lack of agreement is caused by the use of a great variety of aging criteria without a definite knowledge of their respective merits, and also by difficulties involved in attempting to secure marked animals of known age.

Ideally, an evaluation of age determination criteria would be executed by establishing a marked population of known-age animals. The animals would be periodically recaptured in live-traps, and observations on the criteria in question would be recorded. Since each animal's age would be known at the time of a recapture, the measurements for each criterion could be correlated with age. The criterion which was most closely correlated with age would be the most valuable to use as an indicator of the age of other unknown-age animals. This ideal approach is difficult to employ under actual field conditions, because many animals cannot be aged accurately when first captured. Also, it is difficult to establish a nucleus of marked animals such as beavers, because they continually emigrate from study areas.

[1] The Archer and Anna Huntington Wildlife Forest is a property of the State University College of Forestry at Syracuse University. This area, henceforth referred to as the Huntington Wildlife Forest, is maintained and operated for the conduct of wildlife research.

METHODS

To evaluate beaver aging criteria for this study, an attempt was made to secure a population of marked, known-age animals. Altogether, 160 beaver captures were recorded on the Huntington Wildlife Forest. It was observed that some of the animals caught in summer were so small that they were almost certainly born the previous spring. Since most authors (Bailey, 1927; Johnson, 1927; Shaw, 1948; Swank, 1949; Hodgdon and Hunt, 1955) agree that the average date of beaver parturition is near June 1, it was assumed that the very small beavers we captured were born at this time. As an example, three small beavers weighing 6 to 7 pounds were captured in July. We assumed these obviously small and immature beavers had been born June 1, and therefore tallied them as animals from 1 to 2 months old. By good chance, these three animals were recaptured the following October, when they weighed 12 to 14 pounds. Numerous other immature beavers of about the same weight were caught in October. These were almost certainly young animals born the previous spring, and they were assumed to be 4 to 5 months old. A number of other beavers captured during the first few months of their lives were similarly recorded. Thus, some beavers were captured which were obviously young animals. Using these as "known-age" beavers, we had a population containing marked animals of "known age." Thirty of these "known-age" beavers were subsequently recaptured. The evaluation of the three age criteria examined in this paper is based upon measurements and observations made in recapturing these thirty animals in succeeding seasons.

AGE CRITERIA AND AGE GROUPS RECOGNIZED

The three age criteria evaluated are weight, the product of two tail dimensions, and zygomatic breadth. An explanation of a criterion of each factor is presented in the discussion below. In this paper a beaver "kit" is an animal up to and including 12 months old. A "yearling" is an animal 1 year old or in the second year of its life. A 2-year-old beaver is in the third year of its life, while any animal over 36 months old is termed an "adult." This is the nomenclature used by most authorities, and so defined by Buckley and Libby (1955).

Weight

Most authors agree that weight has some value as an age criterion during the first 2 years of a beaver's life, but that it has little value thereafter. Townsend (1953) felt that weight was an excellent criterion for establishing age classes; on the contrary, Osborn (1953) found that weights were of little value in judging age. Data on beaver weights obtained in this study suggest that weight is a very useful aging criterion for the first 2 or 3 years. Thereafter, weight has less value for judging age, since many old beavers weigh no more than 3-year-olds. This fact is illustrated by a beaver which was originally captured in April, 1949. At this time, the animal weighed 42 pounds and was unquestionably an adult. Since its original capture, this adult beaver has been recaptured four times. The five weights of the animal were as follows: April, 1949—42.0 pounds; November, 1953—37.0 pounds; October, 1954—39.0 pounds; October, 1955—38.5 pounds; November, 1957—39.0 pounds. Thus, during a minimum of 9 years of adulthood, this beaver registered no gain in weight. On the single basis of weight ranges as published by several authorities, the animal might well have been erroneously classified as a "2-year-old" upon its first capture.

The weights of beavers believed to be of known age are presented in Table 1. This table is comprised of weights of beavers originally captured at a known age and later recaptured, and it includes beavers up to 2½ years of age. Data from older beavers of known age are not available, because animals around 2 years old normally leave the Forest property. Our failure to recapture these animals corroborates the findings of Bradt (1938), who reported that beavers which are nearing their second birth date leave the parent colony and seek colony sites elsewhere.

Reference to Table 1 suggests that weight of the individual animal is fairly reliable for

TABLE 1.—WEIGHTS OF LIVE BEAVERS BELIEVED TO BE OF KNOWN AGE

Age in Months	Number of Observations	POUNDS		Standard Deviation	Standard Error	Coefficient of Variation (Percent)
		Mean	Range			
2	3	6.4	6.1–6.5	0.24	0.14	3.8
3	3	8.4	8.0–9.2	0.69	0.40	8.2
4	2	11.8	11.0–12.5	–	–	–
5	26	13.7	11.3–17.8	1.74	0.34	12.7
6	13	13.3	8.0–17.5	2.18	0.61	16.4
10 & 11	5	13.0	12.0–15.8	1.57	0.70	12.1
12 & 13	8	15.4	12.8–17.5	1.68	0.59	10.9
16 & 17	5	23.3	20.8–27.3	2.20	0.98	9.4
18 & 19	7	24.9	21.4–28.8	2.72	1.03	10.9
22 & 23	1	21.3	–	–	–	–
24 & 25	2	22.5	22.0–23.0	–	–	–
28 & 29	2	32.3	32.0–32.5	–	–	–

judging age. The standard error remains relatively low throughout the period covered. It is probable that our variation for any given age class results from (1) individual variation, (2) colony site variation, (3) variations in parturition date, and (4) unequal development within the period covered by the same age class. This development is so rapid during the first few months that weight gain within a given month is fairly important. Later in life, weight gain in any one month is proportionately small, and so weights of known-age beavers are listed for 2-month periods in Table 1. It seems likely that parturition dates do not vary enough to cause important weight variations within an age class, except in isolated instances. An example of this kind of variation can be seen in the six-month age group, which includes all kits captured in November. Table 1 indicates that one beaver in this group weighed only 8.0 pounds. This animal may have been born unusually late, and represents the infrequent variation probably caused by an exceptional date of parturition. This particular animal was recaptured a year later, at which time its weight was nearly average for its age group.

The weight data presented in Table 1 emphasize the importance of considering month or season in setting weight standards for a given age group. A kit beaver may weigh anywhere from 1 to 18 pounds, and a yearling beaver may weigh from 13 to 29 pounds. However, this large overlap between age groups definitely does not occur in corresponding seasons. Thus, an October-caught kit weighs from 11 to 18 pounds, while an October-caught yearling weighs 21 to 28 pounds. The values given are extreme observations, not probable weight limits or calculated fiducial limits.

Further reference to Table 1 shows that a winter weight loss is undergone by at least some of the beavers observed. Apparently animals in their first and second summers gain weight steadily through September. By mid-October, beaver food storage has normally started in the Adirondack Mountains, and at that time the transition has been made to a woody diet. Thus, further weight gains in November were not observed, perhaps because of the less nutritious diet and the accompanying activity of food storage. An over-wintering weight loss may occur in some beavers. This may be associated with the amount of available food in the colony site. For example, a yearling beaver in an unusually poor site weighed 25.5 pounds in mid-November. By the following April it weighed only 21.0 pounds. Certainly, little or no weight is gained during the winter months, and a 2- to 5-pound weight loss may frequently occur for any age class.

The heaviest beaver handled during the study weighed 49.0 pounds. Numerous beavers weighing 35.0 to 49.0 pounds were known to be adults, because they were recaptured on several occasions separated by

TABLE 2.—PRODUCTS OF TAIL DIMENSIONS OF BEAVERS BELIEVED TO BE OF KNOWN AGE

Age in Months	Number of Observations	Square Inches		Standard Deviation	Standard Error	Coefficient of Variation (Percent)
		Mean	Range			
2	3	16.1	13.2–17.4	2.51	1.45	9.0
3	2	21.1	21.0–21.2	–	–	–
4	1	27.2	–	–	–	–
5	21	25.9	17.8–33.4	4.18	0.91	16.2
6	12	24.2	17.7–32.4	4.10	1.18	16.6
10 & 11	5	23.1	21.0–26.4	2.74	1.23	11.9
12 & 13	5	26.0	24.2–27.3	1.32	0.59	5.1
16 & 17	5	35.7	31.4–41.9	4.41	1.97	12.3
18 & 19	4	43.5	40.9–48.3	3.31	1.66	7.6
22 & 23	1	39.0	–	–	–	–
24 & 25	2	39.2	36.1–42.2	–	–	–
28 & 29	2	48.8	48.5–49.0	–	–	–

three or more years. Examination of the weights of these adult animals often suggested a slight net weight loss over a period of several years, and very old beavers may weigh less than young adults. There was certainly no evidence that adult beavers became heavier as they grew older.

Product of Tail Dimensions

Haseltine (1950) used the product of the length and width of the scaled portion of beaver tails as an index to age. This measurement, probably the easiest to obtain, appears to have value as a criterion to age. Table 2 lists the products of the tail dimensions of beavers of known age.

The data in Table 2 indicate that a reduction of tail dimension often occurs during the winter months. Thus, this measurement is closely associated with weight, which also displays a winter reduction. Most of the reduction in tail dimensions takes place in the width component, and thus this factor may be more closely associated with body condition or weight than is the length. However, although the length component may be more closely associated with age, it is also subject to greater error in measurement than is the width.

The coefficients of variation of data on body weight and tail dimensions are similar. As might be expected, the ranges of data of tail dimensions are wider than those of weight, with overlapping between a few corresponding age classes. Some of the apparent superiority in precision of the weight

TABLE 3.—WEIGHTS, PRODUCTS OF TAIL DIMENSIONS, AND BREADTHS ACROSS ZYGOMATIC ARCHES OF THREE BEAVERS KNOWN TO BE ADULT

	Beaver No. 1			Beaver No. 2			Beaver No. 3		
	Wt. (lbs.)	Tail (sq. in.)	Zygomatic Breadth (inches)	Wt. (lbs.)	Tail (sq. in.)	Zygomatic Breadth (inches)	Wt. (lbs.)	Tail (sq. in.)	Zygomatic Breadth (inches)
Spring 1949	42.0	–	–	–	–	–	–	–	–
Fall 1949	–	–	–	–	–	–	–	–	–
Spring 1953	–	–	–	–	–	–	–	–	–
Fall 1953	37.0	48.6	–	48.0	64.9	–	39.5	60.9	–
Spring 1954	–	–	–	–	–	–	38.3	60.5	–
Fall 1954	39.0	46.4	–	–	–	–	–	–	–
Spring 1955	–	–	–	–	–	–	–	–	–
Fall 1955	38.5	44.3	3.78	–	–	–	–	–	–
Spring 1956	–	–	–	–	–	–	–	–	–
Fall 1956	–	–	–	44.5	64.9	3.81	35.0	61.0	3.80
Spring 1957	–	–	–	–	–	–	36.0	55.0	3.80
Fall 1957	39.0	44.3	3.81	46.8	63.8	4.03	–	–	–

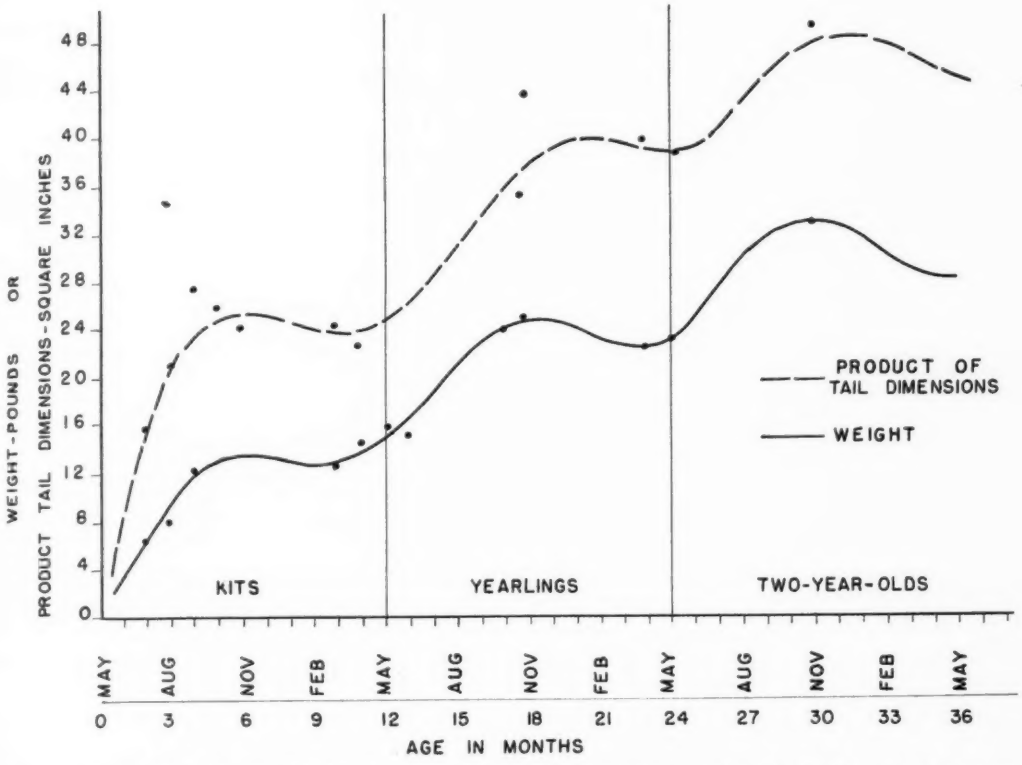

FIG. 1. Comparison of seasonal changes in product of tail dimensions and weight in Adirondack beavers. Actual datum points were obtained by averaging observations for each month.

data is due to the larger quantity of weight information which is available. It seems likely that data on weight and tail dimensions are of approximately equal value in estimating age. Weight data are easily interpreted and visualized, and units of weight are familiar to everyone. On the other hand, dimensions of the tail may be easily obtained in the field, as well as from many trappers who save the tails as souvenirs. Few trappers are willing to obtain accurate weight data; and as some trappers skin their catch at the location of capture, the biologist cannot weigh the furred carcasses at the trappers' cabins.

Figure 1 indicates the approximate relationship between weight and product of tail dimensions. The graphs shown in Fig. 1 are visually drawn to best fit the available data, and are designed only to suggest the relationship between the two criteria. The regression coefficient for the product of tail dimensions is slightly larger than that for weight. At first observation, this might appear to favor the former as an age criterion, since it produces a greater change in value for each advance in age class. On the other hand, most of the difference between the two coefficients results from the first 5 months of age. Thereafter, the slopes are approximately the same.

Table 3 presents data for three beavers known to be adults when captured in 1957. Numerous other animals almost certainly were adults, but these three in particular were known to be adults because they were more than 1 year old when captured in 1953, and were thus 3 years old or more when last captured. In the case of beaver No. 1, the criterion on product of tail dimensions does not clearly separate it from the 2½-year-old beavers in Table 2. However, these same adults are distinctly separated from the 2-year-olds on the basis of weight.

Zygomatic Breadth

Alexander (1951) employed the zygomatic breadth to advantage as an index to muskrat age. Although this measurement is generally associated with prepared skulls, it may be readily obtained from living animals. This is best done with a pair of good quality outside calipers with at least a 6-inch capacity. A tight fit on the zygomatic arch helps to minimize the effect of the layer of thin skin and hair over the bone, and measurements from skulls and from living animals should be approximately the same. In taking this measurement, the zygomatic arch should be measured at its widest point. The calipers have a strong tendency to roll to either side of the maximum arch width, and care must be exercised to prevent this.

Table 4 presents the zygomatic breadths of 30 animals of "known age." The most striking feature of these data is the remarkably low coefficient of variation. This reflects the comparative precision with which the measurement may be made. Unlike the two criteria previously examined, there is no indication that zygomatic breadth decreases during the winter. Of course, this would not be expected of ossified bone. A comparison of Table 3 and Table 4 indicates that the zygomatic breadth measurement can be employed to separate easily an adult from a 2-year-old animal.

More measurements from animals of known age are required to establish firmly zygomatic breadth limits for each age class. With the limited information available, the measurement appears to have considerable potential as an age criterion. Its procurement requires more technical knowledge than obtaining either weight or tail dimensions. However, the measurement is easily obtained by experienced personnel.

DISCUSSION AND CONCLUSIONS

The three criteria examined are all useful for beaver aging, providing the season of observation is taken into account, because the growth rate of Adirondack beavers is not uniform. A beaver which weighs 13 pounds and possesses a tail of 23 square inches may be from 5 to 12 months old. However, if the observation is made in October, it is obvious from the foregoing that the animal is about 5 months of age. Apparently beaver growth is both rapid and uniform from May to October. In October, growth may be slowed by the change to a bark diet or by the greater physical activity of food storage. There is evidence not only that growth ceases during the winter, but that animals may be considerably smaller in spring than in the previous fall. After the ice breaks up and green plants appear, rapid growth once again begins. Hakala (1952) and Buckley and Libby (1955) recognized a change in the growth rate of Alaska beavers during the different seasons, although they apparently did not observe a winter weight loss.

Table 5 summarizes the probable weights, products of tail dimensions, and zygomatic breadths which will be encountered in the four age groups of March- and April-caught Adirondack beavers. Information is presented for this period rather than for the fall, because most examples will be obtained from early spring trapping seasons. In some

TABLE 4.—BREADTH ACROSS ZYGOMATIC ARCHES OF BEAVERS BELIEVED TO BE OF KNOWN AGE

Age in Months	Number of Observations	Breadth in Inches		Standard Deviation	Standard Error	Coefficient of Variation (Percent)
		Mean	Range			
5	6	2.78	2.66–2.88	0.10	0.04	3.6
6	10	2.77	2.63–2.88	0.09	0.03	3.2
10 & 11	1	2.78	–	–	–	–
12 & 13	4	2.88	2.81–3.00	0.08	0.04	2.8
16 & 17	3	3.26	3.20–3.30	0.05	0.03	1.5
18 & 19	3	3.37	3.34–3.38	0.02	0.01	0.4
22 & 23	–	–	–	–	–	–
24 & 25	2	3.42	3.31–3.53	–	–	–
28 & 29	1	3.31	–	–	–	–

TABLE 5.—APPROXIMATE RANGES OF WEIGHTS, PRODUCTS OF TAIL DIMENSIONS, AND ZYGOMATIC BREADTHS OF FOUR ANNUAL AGE GROUPS OF SPRING-CAUGHT BEAVERS

Age Group (age in months)		Weight (pounds)	Product of Tail Dimensions (sq. inches)	Zygomatic Breadth (inches)
March–April Kits (10–11)	Range	12–17	16–28	2.50–3.00
	Average	14	24	2.70
March–April Yearlings (22–23)	Range	20–26	34–42	3.20–3.40
	Average	22	38	3.30
March–April Two-year-olds (34–35)	Range	28–34	43–45	3.50–3.60
	Average	30	44	3.55
March–April Adults (46 or more)	Range	35–	46–	3.65–

cases the data in Table 5 are limited, and the ranges may require modification when further information is available. The weight and tail dimension data agree fairly well with those obtained by Hodgdon and Hunt (1955) from Maine beavers.

Although all three criteria which have been examined are useful for aging live beavers, an individual will occasionally be found which varies markedly from the average for its age class. In such cases, the observer can only apply several aging techniques, using the most frequent age determination for his final result. This will be particularly true where observations are being made in a short period of time on a heterogeneous group of beavers from several locations and site types. However, where beavers from a limited locality are being examined, greater precision should be possible. The findings herein presented apply particularly to the Central Adirondack Mountains, their application to other localities should be made with caution.

SUMMARY

The criteria of weight, product of tail dimensions and zygomatic breadth are all useful for separating live beavers into the four recognized age classes. Data on both weight and tail dimensions are the easiest to obtain, although it is highly important to consider the season when making age estimates from these measurements. This is because body weight and tail size do not develop uniformly through the season, but may fluctuate widely depending upon diet, activity, etc. The zygomatic breadth measurement is most difficult to obtain, but since there is much less variation associated with its use, the season in which measurements are made is of less importance. There is evidence that data on weight and tail dimensions become unreliable for aging old beavers. The zygomatic breadth measurement may be useful for this purpose, although additional research is needed to establish definitely the full value of this criterion.

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LEPTOSPIROSIS AND BRUCELLOSIS SEROLOGICAL REACTORS IN WISCONSIN DEER, 1957–1958[1]

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With 4,200,000 cattle and approximately 600,000 white-tailed deer (*Odocoileus virginianus*) in the state, Wisconsin has begun to give attention to the possible disease problems that can arise from close contact of these two species. Both deer and cattle are distributed in varying numbers among every one of the state's 71 counties. The cattle density is greatest in southern Wisconsin and the deer population is heaviest in central and northern Wisconsin.

The two diseases which have been given initial attention are brucellosis (*Brucella abortus*) and leptospirosis (*Leptospira pomona*). Both are important diseases of Wisconsin cattle, both can infect man, and both have been reported to occur in deer.

Serological evidence of brucellosis in bison and elk was obtained as early as 1932 by Rusk. Subsequent investigations have not only substantiated the serological implication of bison and elk and added moose to the list of hosts, but also supplied evidence of isolation of the causative organism (Katz, 1941; Fenstermacher and Olson, 1942; Jellison, *et al.*, 1953; and Corner and Connell, 1958).

Several serological surveys have been made in the United States to determine the presence and prevalence of brucellosis in deer. Some of these investigators were Bolin, *et al.* (1949), who studied the disease in North Dakota, Wedman and Driver (1957), who studied the disease in Minnesota, and Shotts, *et al.* (1958), who studied the disease in Georgia. All investigators reported that less than 1 percent of the deer tested had a positive titer for *Brucella abortus*.

Leptospires of several serotypes have been isolated from a wide variety of wild mammals (McKeever, *et al.*, 1958; van der Hoeden, 1958; Babudieri, 1958). The first *Leptospira pomona* serological reactors among white-tailed deer were reported from Minnesota by Wedman and Driver (1957). About 16 percent of the animals tested were reactors. Similar surveys have been conducted by state agencies in Michigan (Youatt, *et al.*, 1959), Massachusetts (Reynolds and Smith, 1958), Illinois (Ferris, *et al.*, 1958), Missouri (Anonymous, 1958), Ohio (Goldstein, *et al.*, 1958), Georgia (Shotts, *et al.*, 1958), and Wisconsin (Trainer, 1958). The presence of serological reactors to *Leptospira pomona* in white-tailed deer has been established by these investigations, but the significance of the titers in deer and the role of deer in the epizootiology of the disease is still unknown.

The objective of this serological investigation was to obtain evidence of the prevalence and importance of leptospirosis and brucellosis in Wisconsin deer.

MATERIALS AND METHODS

To obtain satisfactory deer blood specimens for serological testing, several collect-

[1] This work was undertaken with Federal Aid to Wildlife Restoration funds under Pittman-Robertson Project No. W-24-R.

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ing procedures were employed and compared under field conditions.

Blood collecting procedures.—The cooperation of state conservation wardens was enlisted to collect blood samples, from selected road-kill deer, by using procedures as aseptic as possible under existing field conditions. Collections were made from the thoracic cavity in 8-ml. serological test tubes with 2 ml. or more of whole blood sought to obtain the necessary volume of serum for testing. Mailing tubes were supplied the collectors and specimens were sent to the laboratory immediately after collecting.

The utilization of otherwise wasted blood from road-kill deer (over 3,000 during 1958) provided a good statewide collection of blood specimens with a fairly random sex, age and seasonal distribution. Thirty cooperating wardens submitted by mail about 400 deer blood samples during the last 4 months of 1957. However, because of the variation in mail pickups, train connections, and satisfactory holding temperatures, the number of usable samples (71) was relatively small. The majority of losses resulted from hemolysis. Of the usable samples, 50 percent came from four wardens stationed where rapid transportation to the laboratory was available; therefore, this procedure is satisfactory providing there is no delay in transit to the laboratory.

In Wisconsin it is compulsory to present for registration every deer killed during the hunting season either in the county where shot or the adjacent county. State conservation biologists establish deer sexing and aging stations at selected registration sites. Their cooperation was secured to collect whole blood samples when available from field-dressed carcasses presented for registration. The same collecting equipment was provided the biologists as was used by the wardens for road-kills. Similar collecting procedures were used, except that the samples were delivered to the laboratory by automobile within 48 hours of the collecting time.

During the first trial of this method in 1957, 140 of the 310 testable deer blood samples taken were obtained in this manner. In 1958 the majority of the blood samples were collected by this procedure and approximately half of the blood secured was testable. Hemolysis was again the major limiting factor. Holding the samples at a cool, constant temperature appeared to overcome this problem. Information pertaining to the age, sex, and general condition of the animals was collected by the biologists, and increased the value of these samples.

Several controlled deer hunts are held on federal wildlife refuges in Wisconsin each year. All deer taken by hunters in these areas must be processed through established check stations. Federal and state field personnel cooperated in collecting blood from field-dressed animals passing through these check stations. Blood collecting equipment and procedures were identical with those already described. Collection of deer blood specimens during special controlled hunts was valuable when it was desirable to study specific areas; however, this very fact limited the usefulness of the material.

Serological tests.—The presence of brucellosis was determined on the basis of the serum plate agglutination test at the Wisconsin Department of Agriculture Central Animal Diagnostic Laboratory under the direction of Dr. E. P. Pope. The brucellosis serum plate agglutination test of the United States Department of Agriculture was utilized; the antigen used was *Brucella abortus* strain 11193. Serum dilutions of 1:50, 1:100 and 1:200 were employed and reactions of 1:100 or higher were considered positive. The testing techniques and the method of interpreting results were those approved by the Animal Disease Eradication Division of the Agricultural Research Section.[3]

Leptospirosis testing was also conducted at the Central Animal Diagnostic Laboratory and positive reactors were detected in two ways. In some of the 1957 work the Stoenner plate agglutination test, using com-

[3] *Brucella Abortus* Diagnostic Antigen Outline (May 1, 1950 rev.), issued by the Animal Disease Eradication Division of the Agricultural Research Service, 1950.

mercially prepared *Leptospira pomona* antigen[4], was employed. Samples were also tested by the agglutination-lysis technique and the results compared. The live antigen used in the latter test was *Leptospira pomona,* which was grown and standardized at the State Central Animal Diagnostic Laboratory. Testing techniques were identical with those employed by the Wisconsin Department of Agriculture in its cattle testing program. Serum dilutions of 1:10, 1:100, 1:1,000 and 1:10,000 were tested, with reactors of 1:100 or higher considered positive. In cattle, individual leptospirosis reactors with a titer of 1:100 or more are considered significant in nearly all laboratories and indicate past or recent infection with leptospirosis. To diagnose an active infection, it is necessary to consider titer, clinical symptoms, and the herd history. Leptospirosis reactors are known to persist in cattle up to 5 years (Pope, 1959).

RESULTS

Brucella test results.—Over 600 white-tailed deer blood samples taken from 25 counties were tested for brucellosis during 1957 and 1958. Of these, one sample (0.16 percent) yielded a 1:100 reaction. This was a yearling buck taken from an agricultural area of the state.

Leptospira test results in 1957.—During 1957, 110 deer blood samples were tested by both the Stoenner plate agglutination and the agglutination-lysis techniques. A comparison of these procedures showed that the Stoenner plate test detected a varying number of reactors that possessed titers as determined by the agglutination-lysis test: at 1:10, 13 percent reacted; at 1:100, 15 percent; at 1:1,000, 40 percent; and at 1:10,000, 90 percent (Ruedy *et al.,* 1959). As a result, subsequent sera were tested by the more sensitive and informative agglutination-lysis procedure.

Three hundred and ten suitable blood samples out of the 812 collected in 1957 were tested for serological reactors to *Leptospira pomona.* The results by county are presented in Table 1. Approximately 30 percent of all animals tested were positive reactors. Of the 8 counties from which 10 or more of the samples were obtained, 6 had positive reactors, the lowest had 8 percent and the highest 50 percent. The two counties having low deer densities had no reactors. The six counties from which reactors were obtained all had high deer populations. Very little can be concluded concerning counties from which there were less than 10 samples.

In 1957, information accompanying blood samples was sex, age (adult vs. fawn), county where collected, and general comments on the condition of the animal. Table 2 relates this information to the serology. It shows that approximately 36 percent of the 231 adults tested and 13 percent of the 79 fawns tested were leptospirosis reactors. Of the adults tested, 42 percent of the 125 males and 29 percent of the 106 females were positive reactors. This apparent higher prevalence in males than in females is even more

TABLE 1.—DEER LEPTOSPIROSIS SEROLOGICAL RESULTS BY COUNTY[1] DURING 1957

County	No. Usable Samples	Positive	Negative	Percent Positive
Wood	12	8	4	66
Juneau	96	48	48	50
Adams	10	5	5	50
Jackson	72	22	50	30
Dodge	49	9	40	18
Rusk	13	1	12	8
Ashland	2	0	2	0
Buffalo	1	0	1	0
Clark	1	0	1	0
Columbia	3	0	3	0
Dane	2	0	2	0
Dunn	1	0	1	0
Eau Claire	1	0	1	0
LaCrosse	2	0	2	0
Monroe	3	0	3	0
Price	21	0	21	0
Sawyer	2	0	2	0
Sauk	1	0	1	0
Waushara	3	0	3	0
Waupaca	14	0	14	0
St. Croix	1	0	1	0
Totals	310	93	217	30

[1] See Fig. 1 for the location of these counties in Wisconsin. The counties are listed with the highest reactor counties first.

[4] Fort Dodge Laboratories, Inc., Fort Dodge, Iowa.

TABLE 2.—DEER LEPTOSPIROSIS SEROLOGICAL RESULTS BY SOURCE COMPARING AGE AND SEX DIFFERENCES IN 1957

Source	Total Deer	Total Adults	Adult Males	Adult Females	Total Fawns	Fawn Males	Fawn Females
ROAD-KILLS							
No. tested	71	57	25	32	14	6	8
No. positive	10	10	5	4	0	0	0
GUN SEASON							
No. tested	141	114	78	36	27	7	20
No. positive	56	48	35	13	8	0[1]	8
CONTROLLED HUNTS							
No. tested	98	60	22	38	38	13	25
No. positive	27	25	12	14	2	0	2
TOTALS							
No. tested	310	231	125	106	79	26	53
No. positive	93	83	52	31	10	0	10

[1] One male fawn from Juneau County yielded a 1:10 reaction.

striking when one considers that the average age of male deer taken is less than that of females (Table 4), as a result of the Wisconsin buck law. Pre-hunting season counts show that only one out of every six deer is an adult buck (Dahlberg and Guettinger, 1956).

Particularly interesting was the high prevalence of leptospirosis reactors in west-central Wisconsin counties. Included in this area is the 42,000-acre Necedah National Wildlife Refuge, where extremely high deer populations are controlled only by bow and arrow hunting. Fifty percent of the adults tested from this area were reactors, and the high male reactor rate (62 percent) to female (47 percent) was maintained.

Among the limited number of deer tested from agricultural areas in 1957, leptospirosis reactors appeared to be negligible.

Leptospira test results in 1958.—With the 1957 findings in mind, the 1958 deer serological survey was planned. Three types of habitat were selected with varying densities of cattle and deer populations (Fig. 1). Area I is the farm and farm-fringe area with a low deer and high cattle population. Area II is prime deer range in the west-central portion of the state, where cattle populations are relatively low. Jackson County in this area was the number one county in the state for legal gun kill in both 1957 and 1958, with 5,500 and 6,000 deer respectively (6 deer per square mile). The Necedah Wildlife Refuge is located in this area and in 1957 it had a bow and arrow kill of 900 deer (14 deer per square mile). Area III is prime deer range in northern Wisconsin where cattle populations are very low. In 1957 and 1958 Vilas County had a legal gun kill of approximately 3,500 and 4,000 deer (4 to 5 deer per square mile), while in adjacent Oneida County the annual kill approached

FIG. 1. The 1958 study areas for deer leptospirosis, and the deer and cattle populations per square mile.

TABLE 3.—DEER LEPTOSPIROSIS SEROLOGICAL RESULTS BY AREA COMPARING AGE AND SEX DIFFERENCES IN 1958

Area	Total Deer	Total Adults	Adult Males	Adult Females	Total Fawns	Fawn Males	Fawn Females
I FARM							
No. tested	110	89	60	29	21	9	12
No. positive	1	1	1	0	0	0	0
II WEST-CENTRAL							
No. tested	151	122	72	50	29	11	18
No. positive	62	57	37	20	5	0	5
III NORTH							
No. tested	15	13	6	7	2	1	1
No. positive	8	8	4	4	0	0	0
TOTALS							
No. tested	276	224	138	86	52	21	31
No. positive	71	66	42	24	5	0	5

5,500 (5 deer per square mile). Leptospirosis in cattle has never been diagnosed in either of these northern counties, although only limited serology has been conducted because of the sparse cattle population.

Age and sex information was obtained for the animals sampled and these results are summarized with the serology in Table 3. Area I (farm and farm-fringe) yielded only one positive *Leptospira pomona* reactor in 1958. This was a 1.5-year-old male deer. A total of 163 blood samples from the farm counties were examined in 1957 and 1958. The detection of only 10 reactors over the 2-year period indicated that leptospirosis is uncommon among deer in this area. Nine of the 10 reactors found came from Horicon Marsh in Dodge County, a federal wildlife refuge which supports an unusually large deer herd for this farming area.

The west-central area, Area II, with large deer populations had as many leptospirosis reactors in 1958 as in the previous year. A total of 329 blood samples from this area were examined and 137 positive reactors, or 42 percent, were detected. When only adult deer were considered, approximately 50 percent were positive serological reactors.

Area III, representing typical northern deer habitat, yielded only a small number of testable deer blood samples. Hemolysis occurred in over 90 percent of the blood samples obtained. From the limited number of specimens it appears that leptospirosis reactors are present and possibly quite common.

Of the entire group of 276 blood samples tested in 1958, 26 percent were reactors. The percentage is lower than that obtained in 1957; however, the group in 1958 included a large number of deer from agricultural counties in which only one reactor was found. The results from good deer range in 1958 are similar to those obtained in 1957.

Of the 71 leptospirosis reactors detected by the agglutination-lysis technique at the 1:100 dilution or higher, 66 were adult deer and 5 were fawns. Among the adults there were seventeen 1:100 reactors; thirty-one 1:1,000 reactors; and eighteen 1:10,000 reactors. Among the fawns there were four 1:100 reactors and one 1:1,000 reactor. The average reactor titer was 1:1,000. There was no difference in titers between adult male and adult female reactors. Titers did not noticeably increase with age, once the deer had matured.

Ages of the total sample tested, reactors, non-reactors, and average hunting season kills are compared in Table 4. The deer are separated into two age groups. One group includes only 1.5-year-old animals; the other, animals aged 2.5 years or more. This type of grouping separates young adults (1.5 years) from animals which have experienced at least one complete breeding season (2.5+ years). The age of the males tested was less than that of the females; this differ-

TABLE 4.—COMPARISON OF ADULT DEER AGES WITH LEPTOSPIROSIS REACTORS, NON-REACTORS AND AVERAGE HUNTING SEASON AGES IN 1958

Area	Adult Deer			Reactors		Non-reactors	
	Total	Males	Females	Males	Females	Males	Females
I FARM AND FARM-FRINGE							
No. 1.5 yrs.[1]	59	46	13	1	0	45	13
No. 2.5+ yrs.[1]	30	14	16	0	0	14	16
II WEST-CENTRAL							
No. 1.5 yrs.	68	43	25	19	7	24	18
No. 2.5+ yrs.	55	30	25	19	13	11	12
III NORTH							
No. 1.5 yrs.	7	4	3	2	1	2	2
No. 2.5+ yrs.	6	2	4	2	3	0	1
TOTAL SAMPLE TESTED							
No. 1.5 yrs.	134	93	41	22	8	71	33
No. 2.5+ yrs.	91	46	45	21	16	25	29
HUNTING SEASON AVERAGE AGE							
No. 1.5 yrs.	1,035	741	294				
No. 2.5+ yrs.	948	427	521				

[1] The deer were divided into two age groups: one includes only 1.5-year animals, the other 2.5-year and older (2.5+) animals.

ence is statistically significant at the 99 percent level of confidence. The sample of deer population which we tested was representative in respect to age when compared to the ages of average hunting season deer. Reactors, both male and female, are slightly older than non-reactors (not a significant difference), while the difference in age between male reactors and female reactors approaches significance. The chi-square method was employed for statistical analysis.

Cattle and deer populations are related in Table 5 to prevalence of leptospirosis in deer and cattle. Prevalence of leptospirosis appears to be dependent upon population densities of a specific host. All cattle population figures were obtained from the Wisconsin Crop and Livestock Reporting Service. Deer population figures were obtained from the Wisconsin Conservation Department, Deer Research Project Leader. The number of cattle reactors per square mile was obtained from a random survey conducted by the Animal Disease Diagnostic Laboratory (Pope, 1959).

TABLE 5.—DEER AND CATTLE POPULATIONS AND REACTORS IN THE THREE SELECTED STUDY AREAS

Area	Populations Per Square Mile		Reactors Per Square Mile	
	Cattle	Deer	Cattle	Deer
I[1] Farm	106	5–10	7	0.1
II[1] West-central	39	35–45	6	12
III North	3	25–35	0	20

[1] Approximately 30 percent of the cattle herds tested in Areas I and II contained leptospirosis serological reactors.

DISCUSSION AND CONCLUSIONS

During the 2 years of this serological investigation, whole blood samples from Wisconsin deer were obtained from road-kills and from deer shot during regular and controlled deer hunts. Blood collections made by game biologists and wardens at stations established for checking sex and age of deer provided the best samples. Simplicity of collection, speed of delivery to the laboratory, and careful control of holding temperatures appeared to be important factors in obtaining serum specimens suitable for serological studies.

Only one reactor was detected among 600 blood samples from deer tested for the presence of antibodies to brucellosis. It appears that in Wisconsin brucellosis is not an important disease of white-tailed deer.

Leptospirosis reactors were found in Wis-

consin's native deer population in sufficient numbers to lead to the conclusion that leptospirosis is an important disease of deer. Whenever an adequate number of samples were tested from an area with a high deer population, leptospirosis reactors were found. Approximately 28 percent of all deer tested gave a positive reaction (1:100 or higher) with the agglutination-lysis test. The average titer of 1:1,000 for reactors is highly significant for cattle and may be highly significant for deer.

There was a higher prevalence of leptospirosis reactors among adults than fawns. This can be partially attributed to the greater chance for exposure that comes with age. Among adults, there was a higher percentage of reactors in males than in females, which is statistically significant at the 85 percent level, even though the males tested averaged younger in age. These facts lead one to suspect that male deer are either more susceptible or more often exposed to leptospirosis than are female deer. When one considers the nature of the causative organism, its proven affinity for the urogenital tract of cattle, and the sexual habits of the white-tailed deer (including the male's polygamous nature), it appears possible that behavior related to the mating season may be important in the transmission of the disease. Some of the age and sex reactor differences observed might be explained in this way. The fact that all reactor fawns were females also strengthens this possibility, since female fawns can and do breed in Wisconsin during their first rutting season, while male fawns do not (Dahlberg and Guettinger, 1956). Venereal transmission of leptospires has been shown to be important in dogs by van der Hoeden (1958), in *Microtus* by Ananin (1954), and possibly in man by Doeleman (1932).

The winter yarding of deer in Wisconsin is common in the north (Area III), sporadic in the west-central area (Area II), and rare in the south (Area I). This excessive crowding of deer into a limited area provides an excellent opportunity for the transmission of a disease. The yarding frequency of deer and the prevalence of leptospirosis reactors are complementary in the three study areas. Blood samples were secured prior to the yarding period of that particular year. This meant that only adults of the sample had yarding experience which gave additional opportunity of exposure to this group. The transmission of leptospirosis during this period of the year presents an interesting possibility, which demands further investigation.

High population density appears to favor higher prevalence of leptospirosis reactors in both deer and cattle. In agricultural areas, where deer are scattered and few in number, leptospirosis reactors were rare, even though 30 percent of the cattle herds tested at random in the same counties had leptospirosis reactors (Pope, 1959). In areas of high deer density where cattle densities are low and leptospirosis in cattle has never been reported, leptospirosis reactors in deer were common.

The shortcomings of employing *Leptospira pomona* as the only test antigen are appreciated. The possibility of the presence of other serotypes in deer populations (Ferris, *et al.*, 1958), the complicating factor of "paradoxical reaction" (Fühner, 1951), and the simultaneous infections with multiple serotypes are recognized. Despite the fact that using one specific antigen would limit the value of the results, it did provide useful information regarding prevalence of titers and a satisfactory starting point for an evaluation of this malady in Wisconsin deer.

It is realized that this serological approach to leptospirosis in white-tailed deer is a preliminary step in evaluating the significance of the disease in deer. Experimental infection of deer in the laboratory and further field investigations are planned to provide information on the susceptibility, routes of transmission, clinical signs, pathogenesis and the development and persistence of antibody.

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SUMMARY

Three methods of collecting whole deer blood samples for serological examination from Wisconsin white-tailed deer were used. Samples obtained by game biologists and wardens at selected hunting season registration stations provided the best material for serological study.

Only one reactor to *Brucella abortus* was detected among the 600 deer tested. From these results and the reports of other investigators, it appears that brucellosis is not the important disease in white-tailed deer that it is in cattle and has been reported to be in bison, elk and moose.

Leptospirosis reactors were found in deer from all areas with heavy deer populations. The average titer of reactors was 1:1,000.

The number of leptospirosis reactors was greater among adult deer than among fawns. A higher prevalence of reactors was found in adult males than in adult females, but among fawns positive titers were found only in females. The tissue predilection of the disease in other species, the apparent age and sex prevalence of the disease in deer and the sexual behavior of deer fit the hypothesis that leptospirosis transmission among deer is strongly promoted during the rut by the sexual behavior customary in this animal species. This mode of transmission could help explain the apparent independence of the disease in deer and cattle populations, and the occurrence of the disease in whichever of the two species is present in greatest numbers in an area, irrespective of the occurrence of the disease in the other species.

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FOOD COMPETITION AND RANGE RELATIONSHIPS OF MOOSE AND SNOWSHOE HARE IN NEWFOUNDLAND

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Lack of food as a factor in population declines of snowshoe hare (*Lepus americanus*) has been considered, notably by MacLulich (1937) and Grange (1949). Snowshoe hare feeding habits have been examined from the viewpoint of damage to forests, forest reproduction and reforestation by Baker, *et al.* (1921), Wilson (1942), Aldous and Aldous (1944), Cook and Robeson (1945), and Krefting (1953). In 1953, D. H. Pimlott conducted a field study in Newfoundland concerned with damage to forest reproduction by hare and moose (*Alces americanus*). The degree of browsing on a part of the Humber Game Reserve indicated marked competition for food between the two species.

The present study is part of a research program begun in 1954 on the Newfoundland snowshoe hare. The favored browse plants of hare and moose are reported, and an attempt is made to establish the degree of competition existing between these two mammals.

Data were obtained during a limited study in the Sandy River watershed of central Newfoundland (Dodds, 1955) in a broader survey in western and west central Newfoundland in 1956 and 1957, through scattered samplings over the Great Northern Peninsula and Emberly Island, Placentia Bay, and from general observations over the period 1953–58 throughout much of the western interior of the Province.

METHODS

Field work began in mid-June and continued through August. Methods employed during the 1953 portion of the study differed slightly. This fact is considered in the analysis and interpretation of results.

In the 1956–57 study, plots of two sizes, 1/200 and 1/400 acre, were spaced at intervals of 100 or 200 feet along transects 1000 feet apart. Slightly more than 25 miles of line were traversed. Within each plot, all

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woody plants were examined and recorded as to species, size and browsing intensities by moose and hares. Twenty thousand stems were examined in a total sampling area of approximately three acres.

Three general site classes were recognized: *Kalmia* (spruce dominant conifer, ericaceous understory), *Cornus* (fir dominant conifer, ericaceous growth limited), and *Sphagnum* (wet-alder, sedges common).

Four height groups were recognized as follows: I—6 inches to 2 feet; II—2 to 6 feet; III—6 to 12 feet; IV—over 12 feet.

Browsing intensity was interpreted by seven classes: unbrowsed, browsing severe, of medium intensity or light, by moose or hare. In many cases, plants browsed by both animals were recorded twice. Severe browsing was scored when the terminal shoot was removed or more than 50 percent of available browse was taken, or both. Medium intensity consisted of removal of between 10 and 50 per cent of browse within reach of the animal. Light browsing was indicated where less than 10 percent of the plant was browsed. Both old and new browsing on live plants were considered. Dead plants, even if killed by browsing, were not included. Much of this method is modified from that used by Pimlott (1955).

Several factors which could bias the results of the study are: (1) In considering old browsing as well as new, damage to a stem by moose browsing is less likely to heal within a two-year growth period than damage due to hare browsing. (2) Especially in winter, hares may rebrowse an already browsed stem, occasionally to its base. (I believe that moose are less likely to do this.) (3) After the first of July, effects of browsing on hardwoods are more difficult to observe and its is probable that some browsing went unnoticed. (4) A few caribou (*Rangifer caribou terranova*) whose browsing habits overlap those of moose were present in the study areas. (5) Summer browsing by moose does not damage woody growth to the extent that winter browsing does, thus would not always be recognizable especially if it occurred early in the growing season. (6) Early fall frosts often kill terminal shoots of red-berried elder (*Sambucus pubens*). The fragile, dead portions break off readily, and such damage may often be mistaken for the effects of moose browsing. (7) Hare browsing in any area of the study may have been a result of changes in population density not directly connected with species composition, plant succession or competition with moose.

In addition to the field work, hares were kept in captivity by the author at the Cormack field station throughout 1956, 1957, and 1958. Although no feeding experiments were conducted on these animals, observations were made regarding preferences for herbaceous and woody foods, and water consumption was recorded.

FOOD HABITS OF MOOSE

In Newfoundland, moose feed considerably upon herbaceous materials during late spring and summer. In higher areas, where great expanses of sedge and grass marsh occur within a few miles of wooded valleys, moose sometimes graze these grasses and sedges until late in September before turning to a woody diet. In the wooded areas, moose strip leaves in summer, nipping only the most tender tips or terminal shoots of trees and shrubs. By early October, moose are feeding upon the woody portions of trees and shrubs, to a large extent, and resorting only occasionally to the yellowing grasses and sedges. Throughout winter, moose feed upon woody plants, but with the appearance of the first green growth in spring, the diet gradually changes so that by early June it is predominately herbaceous and leafy material.

There are few aquatic areas in Newfoundland which attract high numbers of moose; however, moose do frequent small ponds, lakes and rivers where aquatic growth is present. The only aquatic area used heavily within the limits of the Humber East-White Bay study area may well be the best in Newfoundland. Here, moose browsing was light until late June, heavy during July and decreased in August.

No attempt was made to identify the great number of aquatic or terrestrial her-

baceous plants eaten by moose. Through observation and collection in 1953 and 1954, the following species were frequently noted as being used: pickerel weed (*Pontederia cordata*), bogbean (*Menyanthes trifoliata*), yellow pond lily (*Nuphar microphyllum*), water lily (*Nymphaea odorata*), horsetail (*Equisetum fluviatile*), pondweed (*Potamogeton gramineus*), sedge (*Carex rostrata*), spikerush (*Eleocharis* sp.), meadow rue (*Thalictrum polygamum*), fireweed (*Epilobium* sp.), (*Scirpus cespitosus*) and woods ferns (*Dryopterus* spp.).

In this study at least 35 species of woody plants were browsed by moose. The most important of these are listed in Table 1 for each of three areas studied. Pimlott (1955), in his analysis of the effects of moose browsing upon forest reproduction included yew (*Taxus canadensis*) and mountain holly (*Nemopanthus mucronata*) among the most important. These two species did not occur in quantity in the areas studied by the author. Like fir, aspen is generally a winter food only.

The Humber East-White Bay area supports a high moose density. The dominant coniferous species is balsam fir. The percentage of stems of all species browsed to a height of six feet was 26.2. Twenty-five woody plant species were browsed to some extent. Three species, balsam fir, paper birch and raspberry (*Rubus* sp.) constituted 80 percent of the total moose browsing with balsam fir alone making up 47 percent (Table 1). Fir, raspberry and spruce (*Picea alba*) and (*Picea mariana*) led in availability, constituting 61 percent of the total stems. Thirty-one species made up the remaining 39 percent. Raspberry was taken most readily on more recent cutovers. Spruce was taken only occasionally and probably does not rate as an important moose food anywhere in Newfoundland.

Palatability figures were derived following Hosley (1949) by dividing the percentage available into the percentage used. In this area of quite heavy browsing, there was comparatively little spread within these figures. Red-berried elder, trembling aspen, paper birch, willow, wild raisin, mountain ash, fire cherry and red maple (*Acer rubrum*) were favored species. Although sometimes ranking high in use where they are high in availability, raspberry and speckled alder do not rate high in palatability.

Areas of low browsing pressure exhibit greater variation in palatability measurements no doubt because the animal can more readily select choice foods. Low avail-

TABLE 1.—AVAILABILITY, USE, AND PALATABILITY OF IMPORTANT PLANTS IN ALL STUDY AREAS (MOOSE)

Species	Percent Availability	Percent Use	Palatability Factor
HUMBER EAST-WHITE BAY (11,832 stems)			
Abies balsamea	31.3	47.3	1.51
Betula papyrifera	9.1	20.2	2.23
Rubus sp.	21.0	12.8	0.61
Sambucus pubens	1.5	4.3	2.87
Amelanchier sp.	1.2	2.2	1.83
Prunus pensylvanica	1.0	2.0	2.00
Populus tremuloides	0.6	1.7	2.83
Pyrus americana	0.7	1.5	2.14
Ribes glandulosum	1.2	1.5	1.25
Alnus rugosa	5.3	1.3	0.25
Acer spicatum	0.9	1.3	1.44
SHEFFIELD LAKE (3,238 stems)			
Abies balsamea	17.6	44.1	2.51
Salix sp.	4.3	21.8	5.07
Alnus crispa and *A. rugosa*	2.0	11.2	5.60
Acer spicatum	2.0	5.9	2.95
Rhododendron canadense	19.8	3.8	0.19
Populus tremuloides	0.7	2.6	3.71
Amelanchier sp.	1.2	1.8	1.50
Picea glauca and *P. mariana*	14.3	1.5	0.10
Larix laricina	0.5	1.2	2.40
Rubus sp.	0.3	1.2	4.00
SANDY (2,314 stems)[1]			
Prunus pensylvanica		29.1	
Betula papyrifera		25.0	
Abies balsamea		14.8	
Populus tremuloides		10.2	
Salix sp.		4.6	
Sambucus pubens		3.5	
Myrica gale		3.2	
Cornus stolonifera		2.3	
Amelanchier bartramiana		1.7	
Viburnum cassanoides		1.4	

[1] Use based on species browsed, not total species.

ability of any species tends to raise the palatability factor for that species higher than it might normally be. Both fir and birch were occasionally killed by moose browsing pressure in this study area and in sections adjacent to it.

In the Sheffield Lake area which supports a much lighter moose density compared with the Humber East-White Bay section, spruce and fir are about evenly distributed. No cutting had yet taken place. Ground cover consisted largely of lichen growth in the openings and heavy moss in virgin timber. Ericaceous shrubs constituted over 50 percent of the stems occurring within the plots.

Nineteen woody plant species were browsed to some extent. Three species, balsam fir, willow and mountain alder comprised 77 percent of the total browsed. Lambkill (*Kalmia angustifolia*), rhododendron, balsam fir and spruce comprised 52 percent of the available browse. Twenty-two other species made up the remaining 48 percent. Mountain holly showed a palatability factor of 9.0 but it made up only 0.1 percent of available browse. Willow and mountain alder (*Alnus crispa*) both held ratings of over 5.00.

The Sandy area of central Newfoundland included three burn types—a ten-year-old burn, a three-year-old burn, and an area burned during both fires. All of these areas were cut in the mid- to late 1930's, 8 to 15 years prior to the fires. A sampling of a 10- to 13-year-old unburned cutover is also included in the data. The sample comprised 3,830 stems. Thirty-eight woody plant species occurred within the plots of which 18 were browsed to some extent by moose. Fire cherry, paper birch, balsam fir and trembling aspen constituted 79 percent of the use.

The Sandy area was one of high moose density and an interspersion of annual cutovers provided excellent browse. On the burns studied, about one-third of the stems to a height of 12 feet were used.

Moose prefer to browse on plants they do do not have to reach for, either by bending to their knees or stretching upward. This is evident from the combined data for the Humber East-White Bay and Sheffield Lake areas where the percentage of trees and shrubs browsed up to six feet made up 92 and 99.4 percent of the total browse, respectively (Table 2).

TABLE 2.—HEIGHT GROUP OF TREES AND SHRUBS BROWSED BY MOOSE AND HARES[1]

Height Group	Percent of Total Browse		Percent Browsed of Size	
	Trees	Shrubs	Trees	Shrubs
		MOOSE		
I	52.4	57.5	32.7	9.3
II	39.6	41.9	40.4	26.2
III	6.5	0.6	29.8	3.2
IV	1.5		4.0	
		HARE		
I	59.4	80.3	5.7	9.5
II	35.7	18.3	5.6	8.3
III	3.3	0.7	2.3	2.5
IV	1.6	0.7	0.7	50.0

[1] Based on a sample of 15,070 stems, Humber East-White Bay and Sheffield Lake.

Moose sometimes remain and browse in one area for a considerable time. This trait is equally evident when they are feeding on aquatics, although it is less noticeable when they are grazing. It is probably this tendency to stay within a limited area during a feeding period that provides the evidence observed concerning browsing intensity. Eighty-four percent of all trees browsed and 94 percent of all shrubs browsed were browsed heavily (Table 3), i.e., either the terminal shoots or more than 50 percent of the total stems were taken, or both. This

TABLE 3.—INTENSITY OF BROWSING ON TREES AND SHRUBS[1]

	Trees	Shrubs
	MOOSE	
Heavy	83.7	93.5
Medium	8.7	4.0
Light	7.6	2.5
	HARE	
Heavy	65.9	71.3
Medium	17.4	18.4
Light	16.7	10.3

[1] Based on a sample of 15,070 stems, Humber East-White Bay and Sheffield Lake.

tendency results very often in death of plants in heavily frequented range. Birch is the species most often adversely affected.

FOOD HABITS OF SNOWSHOE HARE

With the first evidence of green herbaceous vegetation, the snowshoe hare abandons a woody diet. Throughout the summer, the diet comprises a great variety of green plant foods as several authors have noted (Seton, 1929; Aldous, 1936; Criddle, 1938; and others). In Newfoundland, wild snowshoe hares are known to feed on wild white clover (*Trifolium* spp.), grasses (Gramineae), sedges (Cyperaceae), ferns (Polypodiaceae), marsh marigold (*Caltha palustris*), and dandelion (*Taraxacum* spp.). Hares in captivity chose clover over any other greens provided.

Hares begin their diet of woody twigs with the first frosts and, after snow arrives, are forced to remain on that diet until spring. At least 31 woody plant species are used to some extent.

Water consumption by captive hares began in the spring when snow disappeared and gradually increased to a peak during July. Consumption did not vary considerably from that reported by Sevaraid (1942), or about one-half pint per day during summer. During winter months captive hares ate snow.

In the Humber East-White Bay area browsing on woody plants began in 10-year-old cutovers and reached its peak in the areas sampled in the 22-year-old cutover. Paper birch, spruce, speckled alder and balsam fir constituted 59 percent of total use. Because of the inclusion of a large sample of cutovers not frequented by hares, the overall use was low and the palatability ratings displayed a considerable spread. Gooseberry, mountain maple, red osier dogwood, mountain ash, shadbush, high bush cranberry (*Viburnum trilobum*), and sweet gale were all favored food species. In this region, but occurring outside the study samples, white spruce was occasionally killed by hare browsing in uncut timber.

In the Sheffield Lake area, 21 percent of the total stems to a height of 6 feet were browsed by hare, suggesting a recent high density. The highly available ericaceous shrubs were heavily browsed. Four species not shown in Table 4 were taken, including gooseberry, larch, wild raisin, and aspen. It is probable that the great abundance of ericaceous shrubs and the extremely low availability of other species tended to limit the number of species taken. Palatability ratings did not exhibit the great spread that was apparent in the Humber East-White Bay areas.

On the Northern Peninsula, plots were studied in five different, widely spaced locations during a period of peak hare density. The overall moose density was low. Within the sample plots, 67 percent of all the stems were browsed by hare. Red osier dogwood, the birches, which included the dwarf species, and mountain maple constituted 68 percent of the use. Although the samples were small, palatability ratings tended to be grouped closely due to the heavy browsing.

No moose occur on Emberly Island. Placentia Bay. It is about one-third of a square mile in area and dominated by copses of dwarfed white spruce and balsam, with heavy growths of compact ericaceous shrubs mixed in. Fir, spruce, lambkill, mountain alder, wild currant, Labrador tea, mountain holly, mountain ash, raspberry, wild raisin, blueberry and white birch are all present. A peak density of hares approximating two hares per acre occurred in 1956, 1 year prior to the time of sampling.

Eighty-one percent of the stems to 6 feet had been browsed here and many of the remaining stems were unavailable because of the dense interlocking growth of limbs which often formed a tough, impenetrable matt. Spruce and fir were browsed to a height of 44 inches where they occurred in fairly open areas. Fir was girdled to this height on the northern end of the island and Labrador tea, birch, blueberry, mountain ash and wild currant were nearly all killed or dying. Due to the practice of pasturing sheep on this island, the scarcity of summer foods may be as important a factor as the lack of a winter food supply in regulating

TABLE 4.—AVAILABILITY, USE, AND PALATABILITY OF IMPORTANT PLANTS IN ALL STUDY AREAS (SNOWSHOE HARE)

Species	Percent Availability	Percent Use	Palatability Factor
HUMBER EAST-WHITE BAY (11,832 stems)			
Betula papyrifera	9.1	22.9	2.52
Picea sp.	10.0	13.2	1.32
Alnus rugosa	5.3	11.6	2.19
Abies balsamea	31.3	11.1	0.35
Acer spicatum	0.9	8.9	9.89
Amelanchier sp.	1.2	4.9	4.08
Rubus sp.	21.0	4.5	0.21
Ribes glandulosum	1.2	4.5	3.75
Ribes lacustre	0.4	4.3	10.75
Pyrus americana	0.7	3.5	5.00
SHEFFIELD LAKE (3,238 stems)			
Rhododendron canadense	19.8	47.0	2.37
Kalmia angustifolia	24.9	16.5	0.66
Abies balsamea	17.6	10.5	0.60
Salix sp.	4.3	4.4	1.02
Vaccinium sp.	3.6	4.1	1.14
Picea sp.	14.3	3.9	0.27
Acer spicatum	2.0	3.6	1.80
Amelanchier sp.	1.2	2.7	2.25
Ledum groenlandicum	3.4	2.4	0.71
Betula papyrifera	2.6	1.4	0.54
NORTHERN PENINSULA (610 stems)			
Cornus stolonifera	28.0	37.1	1.32
Betula sp. (Dwarf or Bog Birch)	7.8	12.3	1.58
Acer spicatum	7.2	11.4	1.58
Myrica gale	17.7	9.7	0.55
Picea sp.	6.3	4.8	0.76
Larix laricina	2.7	4.3	1.59
Ericaceae (mostly *Kalmia angustifolia*)	5.1	4.3	0.84
Amelanchier sp.	3.1	3.4	1.10
Salix sp.	2.9	2.8	0.96
Viburnum edule and *V. trilobum*	2.5	2.3	0.92
EMBERLY ISLAND (139 stems)			
Kalmia angustifolia	40.7	44.0	1.08
Abies balsamea	31.7	30.0	0.95
Picea sp.	16.3	16.0	0.98
Alnus crispa	6.5	6.0	0.92
Ribes glandulosum	1.6	2.0	1.25
Nemopanthus mucronatus	1.6	2.0	1.25

population increases. Hares collected in March, May, July and November 1957, all had some woody material and balsam needles in their stomachs. Stomachs of November-caught hares often contained nearly 100 percent balsam needles. Herbaceous plants were infrequent except in gulleys and moist or grassy areas on each end of the island. Grasses, a few small plots of sedges and rushes, ferns and scattered woodland plants were all cut or grazed almost to ground level. Due to the intense degree of browsing, palatability ratings exhibited very little spread. From the few plots sampled, lambkill, balsam and spruce, in that order, led in both use (90 percent) and availability (88.7 percent). Percentages of height groups browsed by hares are shown in Table 2.

If undisturbed, hares may remain grazing in one spot for a full evening's feeding period. This tendency is also exhibited during winter feeding. During deep snows the hares' movements are quite restricted and coupled with the fact that palatable species may not be as available, suggests an explanation for the intensive use of most plants browsed (Table 3).

COMPETITION

In general, good moose range in Newfoundland is also good snowshoe hare range and, in many cases, marginal range for moose is also marginal for hares. Hares and moose follow a similar feeding pattern. They use herbaceous material considerably in the summer and woody foods during the winter. Both species browse the smaller (and younger) woody plants, concentrating their feeding on plants under 6 feet. Both species also tend to browse individual plants heavily. Of the 30 woody plant species occurring within study plots and browsed by moose, 27 were also browsed by hare. The only important hare foods not taken or taken only occasionally by moose were lambkill and spruce.

In this study, an area of high moose density exhibited low browsing pressure by hare (Table 5). It was also true that what were probably the most dense hare populations encountered during the study were

TABLE 5.—USE OF PLANTS BY HARE AND MOOSE AND RELATIVE HARE AND MOOSE DENSITIES

	Total Stems Sampled	Percent Use Hare	Percent Use Moose	Relative Hare Density	Relative Moose Density
Sandy	3,830	No data	33.0	Very low	Very high
Humber East-White Bay	11,832	4.5	26.2	Low	High
Sheffield Lake	3,238	21.0	12.0	Low	Medium
Northern Peninsula	610	67.0	No data	High	Low
Emberly Island	139	81.0	No data	High	Absent

located in an area of low moose density and on an island where moose did not occur. There were no mammalian predators on the island studied nor was snaring permitted. The island sample was very small but represents the conditions existing there.

Balsam fir is the most important winter moose food in Newfoundland. Heavy browsing on this species during the early years of reproduction on cutovers reduces the hares' winter cover (Figure 1). The effect of terminal browsing on 50 percent of the fir reproduction during these early stages retards growth, allowing winter snows to cover this dominant coniferous species for several years. Hares move into these barren areas during the winter season only occasionally by traversing alder beds or broken stands of residual coniferous growth too poor to have been cut for pulpwood. It is partly this reduction of winter cover by moose browsing which prevents hares from inhabiting an area during the early years following cutting.

Birch is the most important hardwood species for moose and the most important of all species for hares, totalling 20 and 23 percent of all stems taken by moose and hare, respectively. Competition for this species tends to increase after hares begin to inhabit the cutovers to an undetermined point in regeneration around 22 years of age or older (Figure 2). As noted previously where both moose and hare browsed the same stem, that stem was tallied twice. This overlapping on birch resulted in a total use of 117 percent at the 22-year point on the graph. By the time climax conditions are reached, total use has dropped to 38 percent.

Continuous cutting provides highly palatable moose browse in early-age stands interspersed throughout the area. Cutovers up to 13 years of age are browsed heavily by moose and cutovers between 18 and 22 years of age are used to a lesser extent. Browsing in virgin timber is dependent upon interspersion of openings, such as alder beds, streams and ponds, whose edges often provide available palatable browse.

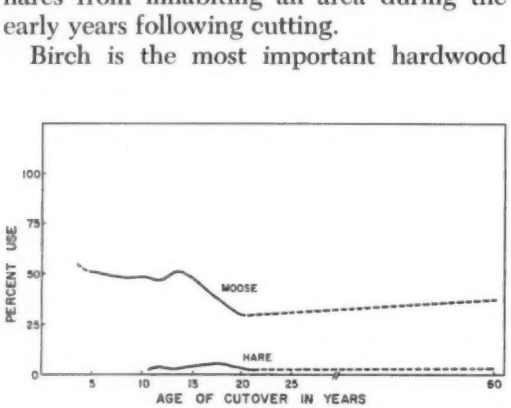

FIG. 1. Browsing on balsam fir by hare and moose indicating heavy use of recent cutovers by moose. Virgin timber figures provided at 60-year point on the graph. Moose moving mean = 3. Hare, actual percent.

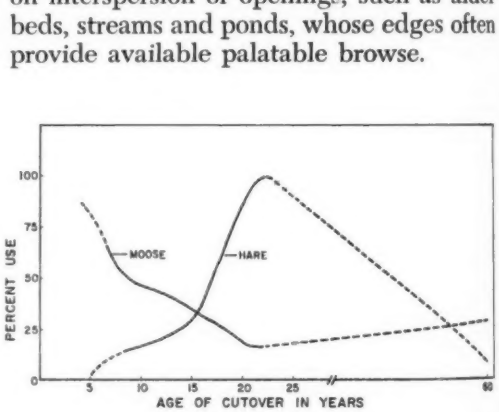

FIG. 2. Browsing on birch by hare and moose in cutovers from 4 to 22 years of age. Virgin timber figures provided at 60-year point on graph. Moose and hare moving mean = 3.

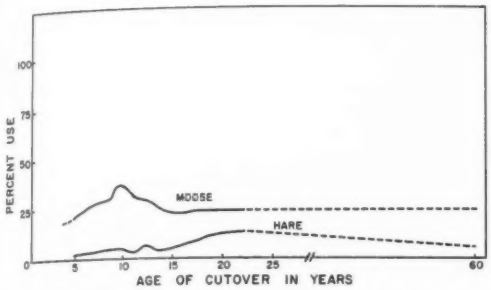

FIG. 3. Browsing on all trees and shrubs by hare and moose in cutovers ranging from 4–22 years of age, and virgin timber. Virgin timber figures provided at 60 year point on the graph. Moose moving mean = 3. Hare, actual percent.

Hares begin to use cutovers later than moose due to the absence of suitable winter cover, and continue to increase their browsing pressure up to at least the 22-year-old reproductive stands. The hares' use of virgin timber is also dependent upon the interspersion of openings. Figure 3 portrays total browsing by both moose and hares in the various age cutovers.

Extensive competition between moose and hares for food probably occurs only in cutover areas of Newfoundland where reproduction is predominately fir. Areas with a spruce canopy and ericaceous understory provide palatable foods for hares not readily taken by moose (Figure 4).

It is possible that heavy moose browsing in areas of predominant fir reproduction have a moderating effect upon hare population fluctuations, tending to maintain near static low densities for a period of ten years or more.

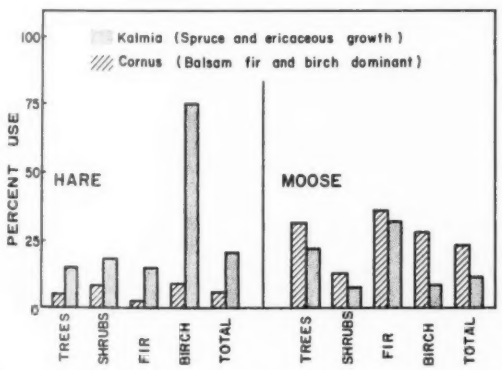

FIG. 4. Percent browsing by hare and moose in "*Cornus*" and "*Kalmia*" sites.

A portion of the Grand Lake area of Newfoundland was one of the first (1926–1930) to be cut for pulpwood in the western portion of the island. In the fall of 1956 the effect of what apparently had been 100 percent use of all available hardwoods by hares was observed. This area no longer exhibited a dense understory, and shrubs or small trees occurred only along old hauling trails and scattered openings. Moose browsing was extremely heavy and the browse line was visible in most openings at varying heights of 7 to 12 feet. Coniferous seedlings 3 inches high were nipped by hare as were bunchberry (*Cornus candensis*) and all available ferns. Spruce occurring occasionally in the openings was killed or misshapen and speckled alder was cut off evenly at a height of 2½ feet, the probable normal snow depth. Winter food is certainly unavailable to the hare in this area now.

SUMMARY

Food habits of moose and snowshoe hare were studied in 1953, 1956 and 1957 in Newfoundland. Areas where competition between the species might exist were given special consideration. Of the 30 woody plant species browsed by moose and occurring within the sample plots, 27 were also used by hares. Both moose and hare feed considerably on herbaceous materials during the summer and depend upon woody plants during the winter.

Both species browse plants under 6 feet most heavily, and tend to browse most plants taken to a high degree of intensity. Browsing of balsam fir by moose retards cover growth for hares in areas where fir reproduction is dominant and may serve to moderate hare population fluctuations. The favored hare food, birch, is also the favored deciduous woody food for moose. Competition for this species reached a peak in the areas sampled in 22-year-old cutover.

It is probable that serious competition between moose and hares occurs only in cutover areas where fir and birch are the

dominant species. In these areas, heavy moose browsing may accelerate the reduction of available hare browse species, creating a winter food scarcity in a 26- to 30-year period.

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BLUE GROUSE PRODUCTION, MOVEMENTS, AND POPULATIONS IN THE BRIDGER MOUNTAINS, MONTANA[1]

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Various aspects of the life history and ecology of blue grouse (*Dendragapus obscurus*) have been reported by Beer (1943), Wing, *et al.* (1944), Buss and Schottelius (1954), Bendell (1954), Caswell (1954), and others. The altitudinal migration has been described by Marshall (1946), Wing (1947), and Bendell (1955a). During winter, blue grouse are reported to be present at higher elevations. In spring, a movement to lower elevations takes place. Broods are raised in the foothills and move to higher elevations in late summer. The present study was on marked blue grouse in the Bridger Mountains in Gallatin County, Montana, to secure information on migrations, brood movements, development of young, population characteristics and general life history. During the summers of 1957 and 1958, 236 grouse were marked. Periodic observations of marked and unmarked grouse were made during other months of the year from April 14, 1957, to October 5, 1958.

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pitality and close cooperation; my wife, Peggy, for encouragement. During the investigation the writer was employed by the Montana Fish and Game Department, under Federal Aid Project W-73-R-2, R-3, and R-4.

DESCRIPTION OF THE AREA

The study area of approximately 10 square miles, on the western slope of the Bridger Mountains in southwestern Montana, is 20 miles north of Bozeman. The main part of the Bridger Range extends in a somewhat north-south direction. The slopes are generally steep (Fig. 1). Elevations on the study area range from 5,200 to 8,840 feet.

Three of four vegetative types described by Wilkins (1957) were included on the study area.

Montane forest (Fig. 1) consisting mainly of Douglas fir (*Pseudotsuga menziesii*) extends from approximately 6,000 to 8,600 feet. Limber pine (*Pinus flexilis*) and white bark pine (*Pinus albicaulis*) are prevalent on the tops of the higher ridges with some alpine fir (*Abies lasiocarpa*) on the north slopes.

Sagebrush-bitterbrush (Fig. 1) occurs on the steep lower slopes, extending from approximately 5,600 to 6,400 feet. Common plants are big sagebrush (*Artemesia tridentata*), bitterbrush (*Purshia tridentata*), Rocky Mountain juniper (*Juniperus scopulorum*), cheatgrass (*Bromus tectorum*), bluebunch wheatgrass (*Agrypyron spicatum*) and balsamroot (*Balsamorhiza sagittata*).

Bunchgrass prairie (Fig. 1) extends outward from the base of the mountain below 5,600 feet. Bluebunch wheatgrass and Idaho fescue (*Festuca idahoensis*) are important grasses. Balsamroot is an abundant forb. Big sagebrush is scattered throughout. The portion not grazed by livestock is devoted mainly to the growing of small grains and

FIG. 1. Blue grouse summer range; foreground, bunchgrass prairie; middle, sagebrush-bitterbrush; rear, lower montane forest.

hay. Deciduous thickets are common along stream courses and at the mouths of draws near the base of the steep mountain slopes. The common shrubs and trees are black hawthorn (*Crataegus douglasii*), common chokecherry (*Prunus virginiana*), Rocky Mountain maple (*Acer glabrum*), black poplar (*Populus trichocarpa*) and rose (*Rosa acicularis*).

METHODS

I spent portions of 41 days in April, May, and June of 1957 and 1958 locating hooting males. I used two mirror-type traps (Tanner and Bowers, 1948) to capture territorial males, and marked four grouse by hurling Christmas tree ornaments filled with lacquer (Bendell, 1954). I searched for nests during parts of 57 days, which overlapped the period of the above activities in May and June of 1957 and 1958.

During portions of 44 days in July and August 1957 and 1958, we cruised the bunchgrass prairie and sagebrush-bitterbrush areas with a jeep. Broods often allowed a close approach. Two men, equipped with hand nets (30- to 36-in.-diameter hoops and 9- to 10-ft. handles) approached from opposing directions netting grouse on the ground, or as they flushed. In late July and August, broods were netted by two observers walking on opposite sides of linear strips of deciduous thickets. A cannon-fired net on a jeep was ineffective on the rough terrain. Modified shorebird traps (Liscinsky and Bailey, 1955) were used in brushy areas for 182 days in 1957 and 1958.

We caught 256 grouse in 1957 and 1958 as follows: 29 adult females, 3 adult males, and 211 juveniles with hand nets; 2 adult females and 9 juveniles in baited traps; 1 adult in a mirror trap; and 1 juvenile with a cannon net.

I weighed grouse of 250 gm. or less to the nearest 5 gm. and those over 250 gm. to the nearest 25 gm. Plumage characteristics were recorded. Wing bands were placed on smaller chicks; aluminum leg bands on the others. Plain and anodized aluminum bands, colored plastic leg bands, painted feathers, and back tags (Blank and Ash, 1956) were used to permit individual identification. We contacted 340 hunters (Sept. 15–29, 1957 and Sept. 21–Oct. 5, 1958) to secure grouse weights, sexes, kill-site elevations, band returns, primary feathers, hunter hours, and numbers of grouse seen and shot by vegetative type.

RESULTS

Breeding

I did not observe displaying males on April 14 or 21, 1957. Between April 28 and May 19, a displaying male was observed on 7 occasions on an area 30 by 75 yards at 6,700 feet. On May 14, a female was on the "territory." The male kept up a continual display similar to that described by Brooks (1926). On May 22, a dead male was found in a mirror trap on the "territory." Five visits, May 25 to June 4, revealed no breeding males on this area.

The latest displaying male was seen on August 2, 1957. Several displaying males were seen in the bunchgrass prairie ½ to 1 mile from the montane forest.

I made more intensive observations in 1958. From March 31 to June 25, eighteen visits were made to a timbered draw, of approximately 17 acres, at an elevation of 5,600 to 6,500 feet. Four displaying males were observed April 19. Three males and one female were marked in this area between May 3 and 11. Observations of marked and unmarked males between May 10 and June 25 indicated a minimum of 7 males present on the 17-acre area. Bendell's (1955a) observations of five males during April and May showed that each male's positions never fell outside a territory of from one to two acres.

Less hooting seemed apparent after the second week of May. Occasional displaying males were seen in the bunchgrass-prairie type. The last displaying male was observed July 30, 1958, at 5,900 feet.

Nests

In the summer of 1958, I found three nests with remains of hatched eggs, in the bunchgrass prairie at distances of 200 yards to over 1 mile from the montane forest. The

first was located between large rocks adjacent to a clump of chokecherry. The second was found under sparse bunchgrass and rose, 20 yards from a chokecherry clump, and the third was hidden under a juniper. "Clocker droppings" indicative of nesting (Bendell, 1954) were found at 7,400 feet. In June of 1958, two recently hatched broods were found in the montane forest at 6,200 feet. Heebner (1956), in reviewing various studies, stated that nests have been found from timberline down through the open sage plains.

Hatch

I estimated hatching dates from primary wing-feather development which is similar to that described by Bump, *et al.* (1947) for ruffed grouse (Caswell, 1954). One chick banded in the present study, at less than 1 week of age, and two chicks banded at the initial flying age (Bendell, 1955) of 2 weeks, were recaptured 6–7 weeks after banding. Bump's method indicated ages 1 week more for each bird than the ages indicated by the banding records. Thirty-two additional juveniles of various ages were captured two to six times each and aged by the Bump method. Hatching dates were calculated from each date on which a bird was recaptured. Recaptures of 8 of the 32 birds occurred before 9 weeks of age. In seven of these eight, the different hatching dates assigned to each bird did not vary over 1 week. Greater variance was apparent with older juveniles. Bump's method was used through the eighth week of age to approximate hatching dates. In 1957 and 1958, hatching dates ranged between May 25 and July 14. In 1957, 80 percent of 49 broods hatched between June 9 and July 6. In 1958, 93 percent of 71 broods hatched between June 8 and 29. The peak of hatching occurred the third week of June in both years.

Growth Rates

Twenty juveniles, weighed from two to seven times each (Table 1) at various ages, provided information on growth. All were initially captured at 8 weeks of age or less. Major gains were attained by 10–11 weeks. Juvenile males weighed more than 1,000 gm.

TABLE 1.—AVERAGE WEIGHTS OF 20 BLUE GROUSE JUVENILES WEIGHED AT VARIOUS WEEKLY INTERVALS

Weeks of Age	WEIGHT (GRAMS)	
	Males	Females
1	–	–
2	95(2)[1]	–
3	150(2)	140(2)[1]
4	–	200(2)
5	350(3)	292(3)
6	444(4)	381(4)
7	650(1)	500(1)
8	650(2)	544(4)
9	819(4)	705(5)
10	1075(1)	767(3)
11	1050(1)	800(1)
12	1067(3)	–
13	1088(2)	–
14	–	850(1)

[1] Number of birds weighed.

and juvenile females ranged between 650–875 gm. by that age. Three chicks, only a few days old, each weighed 25 gm. or less. Average growth rates of approximately 90 gm. and 60–80 gm. a week occurred for males and females, respectively, during the first 11 weeks. For the initial 15 weeks of growth, Bendell (1955c) calculated rates of approximately 60 and 50 gm. per week for males and females, respectively, and stated they were similar to values found by Wing, *et al.* (1944). In those studies on dead birds, variations in hatching dates were ignored and crop-content weights were excluded.

The average weights of 34 juveniles in 1957, at ages of about 10–15 weeks were 983 (775–1,175) gm. for 17 males and 797 (600–975) gm. for 17 females. Average weights for juveniles in 1958, at ages of about 11 to 16 weeks, were 1,008 (850–1,175) gm. for 50 males and 821 (625–1,000) gm. for 61 females. Two yearling males captured in June and July of 1958 weighed 1,125 and 1,225 gm., respectively. Weights of five yearling females in July and August ranged between 775 and 925 gm. Bendell (1955c) recorded average weights of males and females without crops (at approximately 15 weeks of age) as 885 (±50) gm. and 725 (±35) gm. respectively, and average year-

TABLE 2.—LOCATION BY COVER TYPE OF 351 BROOD OBSERVATIONS DURING 1957–1958

Vegetation Types	July 1–15	July 16–31	August 1–15	August 16–31
Montane forest	1	6	11	8
Sage-bitterbrush	4	11	23	3
Deciduous thickets	13	59	72	71
Grass-forbs	23	35	9	2

ling weights in May, June, and July as 1,110 (±40) for males and 790 (±10) gm. for females.

Cover Used by Broods

I made a total of 154 and 217 brood observations during 1957 and 1958, respectively (Table 2), mainly between 5,200 and 6,200 feet. More time was spent in areas where grouse were most abundant. In early summer, broods were often observed in grass-forb areas where balsamroot was a dominant. This association of broods with balsamroot was reported by Heebner (1956), Schottelius (1951), and Wing, *et al.* (1944). By the fourth week of July, desiccation of plants of the bunchgrass prairie—particularly forbs—and increased use of deciduous thickets became apparent.

Return to Former Summer Range

Bendell (1954) discussed the possibility of young returning to the region of their birth. In the present study, a banded male was recaptured on July 21, 1958, at a point slightly more than ¼ mile from where he was banded as a chick on July 24, 1957. A banded female and two of her brood were captured on July 23, 1958, at the exact clump of brush where she had last been observed as a banded chick on August 22, 1957. All 7 observations (3 in 1957, 4 in 1958) of this female were made within approximately the same ½-mile area.

Summer Brood Movements

I made 56 recaptures involving 35 juveniles (one captured 8 times) and 130 observations (1–7 per bird) of 65 marked individuals. Observations of members of 8 broods were sufficient to indicate summer movements. These movements, covering periods of 19 to 47 days during July to September, were restricted to areas with maximum diameters of 440 to 1,320 yards, but most were restricted to one-half mile or less. Bendell (1954) reported similar observations. Five ranges were along linear strips of deciduous thickets and three were along the base of the mountain (Fig. 1).

Broods of two marked females were seen intermingled on several occasions and had nearly identical summer brood ranges. The broods of two marked females appeared to frequent the same deciduous thickets. Other observations of marked and unmarked grouse indicated use of these same areas by other broods. One marked juvenile was identified with two different hens.

Fall Dispersal

There were indications that males and broodless females moved from summer ranges prior to fall dispersal of broods. The latest observation of an adult male on summer range was August 2, 1957. Two marked yearling males, observed 3 to 4 times each on summer range in June and July, were last seen on July 21 and 29, respectively. Numerous observers have stated that adult males initiate upward movement. An apparently broodless, marked hen was observed on July 21, 24, 28, 1958 only on summer range.

Observations of three broods with marked individuals on August 23, 29, and 31, respectively indicated movements away from summer range. Break-up of broods appeared to be concurrent with fall dispersal. An increasing number of singles and small groups of juveniles was observed during late August and September. Of three banded brood mates last seen together August 21, one was shot September 21, 1958, over 3 miles from and 1,000 feet higher than the other two, which were shot 400 yards apart on September 22 and 28, 1958, respectively. Wing, *et al.* (1944) and Bendell (1955a) stated that the earliest break-up in brood organization occurred in late July.

The number of brood observations on the summer range began to decrease the second week and decreased sharply the fourth week of August (Table 3). During late August and September observations of marked

TABLE 3.—AVERAGE NUMBER OF BROOD OBSERVATIONS PER DAY BY WEEKLY PERIODS, BEGINNING WITH THE FOURTH WEEK OF JUNE

Month	Week	1957		1958	
		Number of Days Observing	Average Brood Observations Per Day	Number of Days Observing	Average Brood Observations Per Day
June	4	2.5	0.0	2.0	1.0
June–July	1	2.0	1.5	3.0	1.7
July	2	3.5	2.0	4.0	4.5
July	3	4.0	3.5	4.5	4.7
July	4	4.5	4.7	4.5	6.0
July–August	5	5.0	6.4	4.5	5.6
August	1	5.0	6.6	4.5	8.7
August	2	2.0	5.5	4.5	6.9
August	3	4.5	4.7	4.5	7.3
August	4	4.5	2.0	3.0	3.3
August–September	1	2.5	2.0	1.5	2.0
September	2	1.5	1.0	2.0	1.0

grouse indicated increased abandonment of summer range and an increase in lateral movement. Dates on which 11 marked broods were last seen on summer range were from August 4 to September 5. Only 8 of 23 banded birds shot were on summer brood range; the latest date was September 22. The extent of dispersal was suggested by hunter band returns (Fig. 2); lateral movements up to 2.1 miles and altitudinal movements up to 3.4 miles were recorded.

A somewhat different distribution during the two hunting seasons was indicated. During 1957, the altitudinal migration seemed to have progressed further. In 1957, three hunter band returns showed an average movement of 2.3 miles (0.7 to 3.1) and an average increase in elevation of 1,900 feet (400 to 2,800). Three returns with no elevation changes indicated average movements of 0.4 miles (0.1 to 0.5). In 1958, 10 hunter band returns showed an average movement of 2.0 miles (1.0 to 3.4) and an average increase in elevation of 1,200 feet (400 to 1,600). Eight returns with no elevation changes indicated average movements of 0.6 miles (0.0 to 2.1). Although broods appeared to have left summer brood ranges at about the same time each year, more grouse appeared to be present at intermediate elevations during 1958. This is also probably reflected in the improved hunter success of 1958. Beer (1943) and Marshall (1946) concluded that the upward movement in fall was a response to

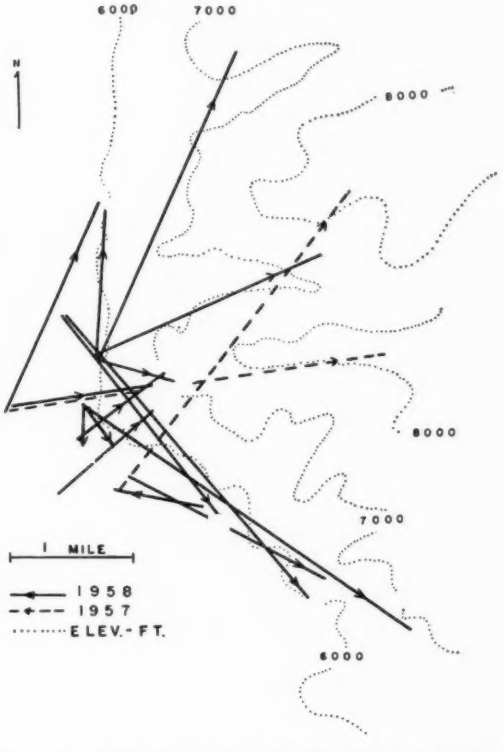

FIG. 2. Fall dispersal and altitudinal migration of blue grouse as indicated by band returns. (Arrows indicate distance between banding site and band return location.)

the ripening of fruit at higher altitudes. Fowle (1944) suggested that the coincidence of the altitudinal movement and berry ripening may well have been accidental. Wing (1947) attributed the movement as a response to a geotropism. Bendell (1954) suggested desiccation of lower vegetation as a factor affecting upward migration. Heebner (1956) stated that there appeared to be more available food on the summer range at the time of the upward movement than there was at the higher elevations. In this study, the upward movement of broods and unavailability of berries at low elevations appeared somewhat linked in 1957, but in 1958 heavy crops of chokecherries were evident on parts of the abandoned summer brood range. The abundance of such food as low red huckleberry (*Vaccinium scoparium*) at higher elevations may have had some effect on the distribution of grouse after altitudinal migration had begun.

Populations

During 1957 and 1958, 255 grouse were captured on approximately 3 square miles of summer range. One square mile of this was subjected to more intensive field work. From July 11 through August 15, 1957, the hens of 6 broods plus 69 juveniles, and from July 1 through August 15, 1958, the hens of 14 broods plus 103 juveniles were banded there. Field observations indicated that in 1957 and 1958 approximate minima of 27 and 34 broods, respectively, had all or part of their summer brood ranges on that 1 square mile. Although broods observed had from one to eight young, few reliable brood size counts were obtained.

Of 104 grouse captured in 1957, 11 died during capture and 6 were discovered later as predator losses. All known instances of predation (including 3 unbanded birds) occurred at a time when broods were concentrated in deciduous thickets and fall dispersal had begun. Evidence of predation was found between August 8 and September 4. Of the remaining 87 banded birds (9 adult females and 78 juveniles), 6 (7 percent) were reported shot. All were juveniles. During 1958, two yearlings (banded in 1957) were recaptured, two grouse with 1957 bands were observed but not identified, and the 1957 bands of two grouse were found on the study area. The number of 1957 marked grouse observed in 1958 possibly was influenced by the habits of yearlings, especially males. Buss and Shottelius (1954) and Bendell (1955a) reported that many yearlings probably do not return to the summer range the first year. No 1957 bands were returned during the 1958 hunting season.

Of the 151 grouse captured in 1958, 10 died during capture and 2 were predator losses. These two losses as well as those of three unmarked birds apparently occurred at the time of fall dispersal. Evidence of predation was found between August 5 and September 4. Of the remaining 139 banded birds (17 adult females, 3 adult males, 119 juveniles), 17 (12 percent) were reported shot. Included were 15 juveniles and 2 adult females.

Evidence from banding data suggested concentration of broods on a relatively small summer range, subsequent dispersal to a large winter range, and a substantial turnover rate the first year of life. Bendell's (1955b) population study indicated heavy loss of blue grouse young (67 percent mortality of chicks by August) and a relatively uniform death rate of adults (31 percent yearly death rate of males). Numerous other studies, including those of Leopold, *et al.* (1943) on pheasants and Errington (1945) on bobwhite quail, have indicated a high turnover rate on other gallinaceous birds. The percentage of banded blue grouse shot (7 percent in 1957 and 12 percent in 1958) indicated the minor influence of hunting.

Indications are that hunting success could be substantially affected by the timing of the hunting season. It was apparent that altitudinal migration was well under way during both the 1957 and 1958 hunting seasons, but was farther along in 1957. In 1957, an average of 5.9 man hours per bird bagged were expended compared to 3.5 for 1958. This difference was interpreted as being

more of a direct result of altitudinal migration than differences in grouse abundance between the two years. In 1957, of 38 grouse (for which the kill-site elevation was available), 25 (66 percent) were shot above 7,400 feet. In 1958, of 120 grouse, only 17 (14 percent) were shot above 7,400 feet. Information obtained from hunters indicated an increased vulnerability of grouse at lower elevations. In 1957, 63 of 289 (22 percent) grouse reported flushed in mountain timber areas were bagged, and 23 of 39 (59 percent) flushed in lowland brush were bagged. In 1958, 108 of 404 (27 percent) grouse reported flushed in mountain timber were bagged, and 51 of 122 (42 percent) flushed in lowland brush were shot. Hartkorn (1957) reported that probably less than 10 percent of blue grouse mountain habitat is ever covered by hunters.

Hatching data for 1957 and 1958 indicated that mid-September seasons harvested juvenile blue grouse mainly at the 12th, 13th, 14th, and 15th weeks of age. Growth-rate data indicate that only relatively small gains in weight would be lost by harvesting juveniles at the 10th, 11th, 12th, and 13th weeks of age.

SUMMARY

During 1957 and 1958, a study of blue grouse was carried on in the Bridger Mountains of southwest Montana. Information was obtained on seasonal movements, development of young, population characteristics and general life history.

Observations during the breeding season indicated a minimum of 7 males present on a 17-acre area. The sites of three nests are described. Hatching dates, determined by ages of juveniles, ranged between May 25 and July 14. The peak of hatching occurred the third week of June for both years. Growth-rate information was obtained from 20 juveniles.

Observations of marked broods indicated movements within approximately a ½-mile area on the summer brood range. During both years dispersal from the summer brood range became evident in August and upward altitudinal migration was well under way by the opening of the hunting season in mid-September. Lateral movements up to 2.1 miles and altitudinal movements up to 3.4 miles were recorded. Seven and 12 percent return of banded birds occurred during the hunting seasons of 1957 and 1958, respectively. No 1957 bands were returned in 1958, and hunting was interpreted as a minor influence in yearly population turnover. Indications were that hunter success could be substantially affected by the timing of the hunting season. Data presented for 1957 and 1958 indicated that the progress of altitudinal migration had a pronounced effect on hunter success.

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INFLUENCE OF DEER ON VEGETATION OF THE APOSTLE ISLANDS, WISCONSIN[1]

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The activities of the white-tailed deer (*Odocoileus virginianus*) have presented a serious problem in northern Wisconsin and adjacent areas for the past two decades. Overpopulations and resulting deterioration of deer habitat have resulted in attempts to control the deer herd through liberalized hunting regulations. The resulting controversy among sportsmen, resort owners, and the state conservation departments indicates the necessity for a study of all aspects of deer-vegetation interrelations, so that persons interested in the future of deer in the region will have a body of well-documented knowledge upon which to base future decisions. This study considers some aspects of the problem of the influence of the deer on the vegetation.

The Apostle Islands, situated at the northern tip of Wisconsin in Lake Superior, are an ideal location for the study of the effect of deer on vegetation. The islands are mostly uniform in topography and soil, but have widely differing deer herds. Some of the islands exceed the surrounding mainland in numbers of deer per unit area;

[1] This study was conducted in cooperation with the Wisconsin Conservation Department and was financed with Federal Aid to Wildlife Restoration funds under Pittman-Robertson Project Number W-79-R.

others have no deer at all, and various intermediate densities of deer are present on other islands. It is therefore possible to deduce from the condition of the vegetation on these islands some of the effects of varying degrees of deer pressure.

It should be noted that the authors are botanists, and their primary concern was the study of the vegetation of the region. The data presented are derived entirely from the vegetation. No data were taken on size of deer herds or on any other aspect of the deer problem except the influence of deer on the vegetation. The results provide basic information of interest to wildlife managers as well as plant ecologists on the dynamics of the interactions of biota in the northern conifer-hardwoods region.

Scientific names of plants follow Gleason (1952). Those of mammals follow Miller and Kellogg (1955).

LITERATURE REVIEW

Deer damage to vegetation in Wisconsin has been studied in an extensive, two-year survey by the state Conservation Department. Two reports (DeBoer, 1947, and Swift, 1948) summarize the results of their survey. The related problem of forest reproduction has been studied by Graham (1954), Switzenberg, *et al.* (1955), and Stoeckler, *et al.* (1957). All the above authors generally agree that hemlock (*Tsuga canadensis*), white cedar (*Thuja occidentalis*), and yellow birch (*Betula luteà*) are adversely affected by deer, while balsam fir (*Abies balsamea*) and sugar maple (*Acer saccharum*) tend to increase with light to moderate deer activity.

Evaluation of carrying capacity of a given habitat for white-tailed deer has been a difficult problem. The problems involved in obtaining an accurate census of deer herds need not be elaborated here, and variations in the quantity and nutritive value of the food supply add to the difficulty of habitat evaluation. Studies of the deer themselves, of their physical condition (Park and Day, 1942) and their fertility (Cheatum and Severinghaus, 1950), have been tried in evaluating range condition. However, these methods do not take into account the nature of vegetational change, and range that is deteriorating rapidly may nevertheless temporarily provide abundant food.

Aldous (1944) has presented a subjective method of evaluating habitat conditions by the condition of vegetation. He has classified range into three categories, understocked, properly stocked, and overstocked, by methods which depend on the experience of the observer for accuracy. Christenson (1954) has made a detailed study of the vegetation of winter range of deer in northern Wisconsin. He has separated his stands subjectively into deer yards (moderately to heavy used) and non-yards (lightly used), and has compared vegetational differences. His work suggests a technique similar to that used in grassland management (Dyksterhuis, 1949) for evaluating grazing lands, using as plant indicators increasers, decreasers, and invaders. Cottam and Curtis (1956a) have developed a list of increasers, decreasers, and invaders for northern Wisconsin deer yards which can be used to give a quantitative assessment of deer damage. The history of Wisconsin deer populations and a statistical summary of records pertaining to deer management have been presented by Bersing (1956). Dahlberg and Guettinger (1956) have summarized the many aspects of the Wisconsin Conservation Department's research findings on white-tailed deer.

DESCRIPTION OF AREA

The Apostle Islands consist of 22 islands in Lake Superior, around the Bayfield Peninsula of northern Wisconsin, ranging in size from a few acres to over 13,000 acres (Fig. 1). Oak Island rises to a height of 480 feet above lake level, but other islands are relatively low and flat, most of them less than 50 or 75 feet above lake level.

The islands lie in the hemlock-white pine-northern hardwoods forest region of

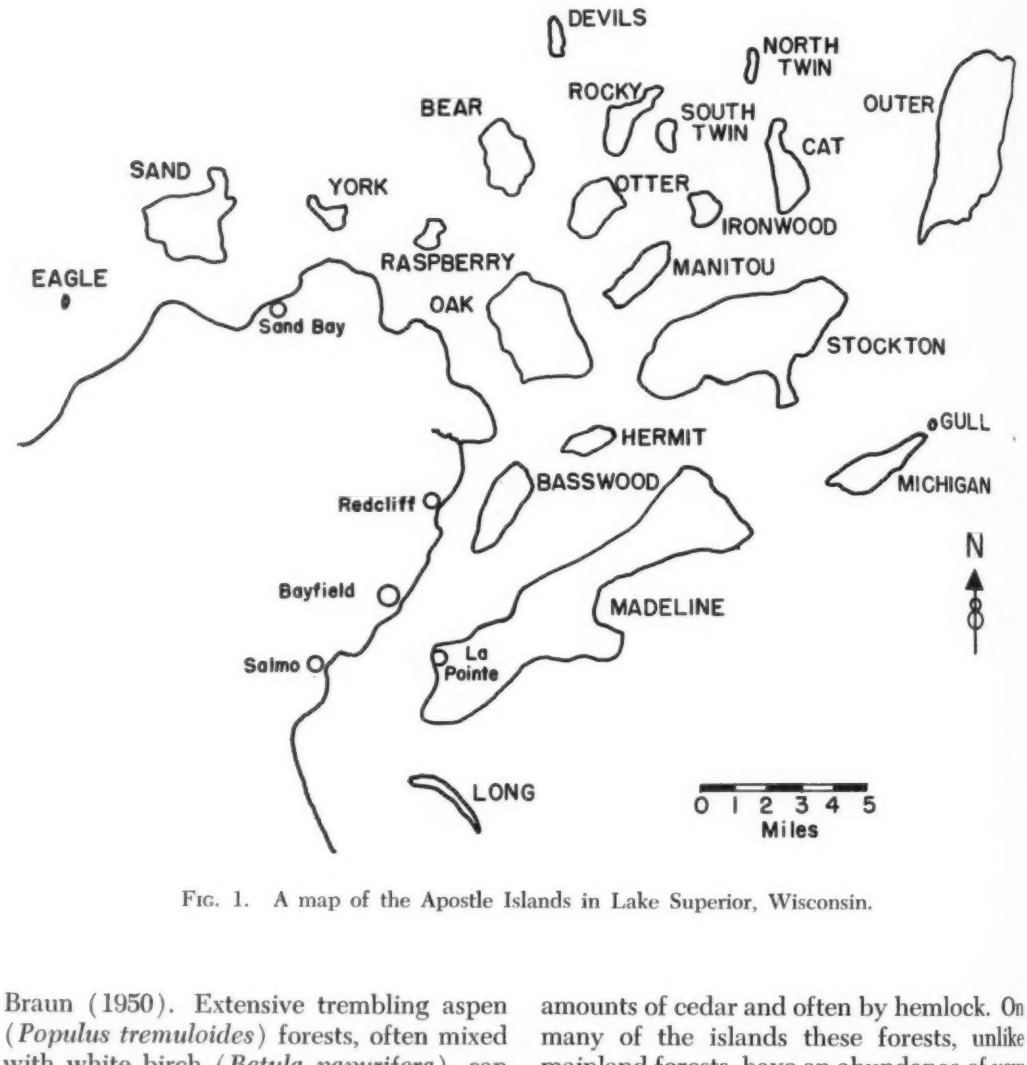

FIG. 1. A map of the Apostle Islands in Lake Superior, Wisconsin.

Braun (1950). Extensive trembling aspen (*Populus tremuloides*) forests, often mixed with white birch (*Betula papyrifera*), can be found on Stockton, Oak, Madeline, Outer, and Basswood Islands. Red, white, and jack pines (*Pinus resinosa, P. strobus, P. banksiana*) are found in one large stand on Madeline and smaller areas on Stockton, Outer, and Cat, and as scattered individuals in other forests. There are well-developed hemlock stands on Madeline, Oak, and especially Outer Islands. The conifers, balsam fir, and white cedar are found on most of the islands. Northern hardwoods, i.e., sugar maple, yellow birch, and some white birch, compose the most widespread forests on these islands, accompanied usually by large amounts of cedar and often by hemlock. On many of the islands these forests, unlike mainland forests, have an abundance of yew or ground hemlock (*Taxus canadensis*) in the understory. Red oak (*Quercus borealis*) is common on a few areas on Oak Island. There are conifer swamps on Madeline, Stockton, and Devils Islands.

Some islands, such as Basswood, Hermit, Madeline, and possibly Oak, have had long-established deer herds. Others have been invaded by deer rather recently, such as Stockton, and even more recently, Rocky and South Twin. Outer, North Twin, Devils, York, Raspberry, and Sand are not known to have had permanent populations, although the last three do have wandering

deer occasionally. Populations vary from light density on Cat and Michigan to moderate on Bear, Manitou, and Otter, to heavy on Rocky, Hermit, Basswood, South Twin, Stockton, Oak, and Madeline Islands.

Predators of deer are scarce. There are reports of timber wolves (*Canis lupus*) on the islands. Coyotes (*C. latrans*) and feral dogs (*C. familiaris*) may take a small toll of deer. Black bear (*Euarctos americanus*) are relatively common and may occasionally take a deer also, especially one that is ill.

METHODS

Seventy-six forest stands were studied during the summers of 1956 and 1957 in the area as follows: Basswood Island 1; Bayfield Mainland 1; Bear Island 3; Cat Island 4; Devils Island 3; Hermit Island 3; Madeline Island 5; Manitou Island 2; Michigan Island 6; North Twin 1; Oak Island 9; Otter Island 3; Outer Island 13; Raspberry Island 1; Rocky Island 6; Sand Island 4; South Twin 3; Stockton Island 7; and York Island 1.

The stands were selected to give a representative sample of the forests of the Apostle Islands, with emphasis on the less-disturbed vegetation. All were relatively free from recent human disturbance. An attempt was made to find areas large enough for sampling which were also homogeneous as far as dominant trees were concerned.

Sampling of trees, saplings, and browse species was done by the quarter method described by Cottam and Curtis (1956). The herbs and shrubs were sampled by means of 3.3 by 3.3 foot (1/4000 acre) quadrats. Data were taken at 40 points in each stand, except in a very few cases where small size or extreme invariability of the stand seemed to justify a smaller sample. Points at which samples were taken were located by paced compass lines. Data on the woody species were taken at each point, while quadrats were sampled at every other point. Frequency data only were taken in the quadrats. Quarter method data were taken for all trees over 12 square inches basal area (about 4 inches diameter at breast height), for saplings (trees between 1 inch diameter and 12 inches basal area) and for browse. Browse in this paper is used to mean any woody stem bearing foliage between the heights of 1 foot and 7 feet.

Each stem of browse in the sample was classified subjectively into one of five categories according to the degree of damage caused by browsing: no browsing, light browsing, moderate browsing, heavy browsing, and total browsing. In the last-mentioned category only stems with some indication of life were counted as available browse. No way of objectively determining damage to the browse has been worked out.

Browse stems were analyzed in several different ways. The relative density (number of stems of a species divided by the total number of stems of all species $\times$ 100), the relative number of stems in each browse damage category, and the minimum density were obtained. Minimum density is a measure of density per acre obtained from the distances taken with the quarter method. It has been shown that, when plants are distributed at random, the average of the quarter method distances is directly related to density (Cottam and Curtis, 1956). To obtain density per acre, these distances are averaged, and the square of the average is divided into the number of square feet in an acre. When plants are clumped rather than randomly distributed, as is the case with some browse species, this relationship no longer holds, and the density obtained is somewhat less than the true density, the degree of error varying with the degree of clumping of the browse. One restriction applies to the interpretation of the minimum density figures for some of the stands. On favorable sites yew grows in almost impenetrable thickets and occasionally reaches a height of over 8 feet. The general aspect of yew in these stands is that of a dense tangle of stems. The difficulties involved in sampling the understory of these stands by any method are very great. With the quarter method, many points were sampled in which all distances were recorded as zero. It is possible under these circumstances that the density of the understory has been overestimated.

In the course of analysis of the data sev-

eral numerical indices were worked out to facilitate description of the deer–vegetation interrelations. The first of these is a browse condition index. It is calculated by multiplying the relative density of browse in each browse damage category by a number ranging from 0 to 4: percentage browse undamaged was multiplied by 0, lightly browsed by 1, moderately browsed by 2, heavily browsed by 3 and totally browsed by 4. These products were then summed and divided by 100, giving values ranging from 0 to 4, depending on the total amount of damage found. A value of 4 would indicate that all stems sampled were totally browsed.

The browse condition index has the obvious limitation that it does not take into consideration the quality of browse present. Were deer given free choice, they would likely do more damage to stands containing a high proportion of choice food than to stands composed mostly of poor food. A stand preference rating was therefore calculated. The species present were divided into groups of first, second, third, or fourth choice deer foods (Table 1), according to the listing of Dahlberg and Guettinger (1956). Several species of the present study were not included in this list, and values were assigned to them according to their apparent value in the stands studied. The quantity of these species was very small and therefore their values had little effect on the total picture of a stand. The preference rating of a stand was derived by multiplying the relative density of first choice food by 1, that of second choice food by 2, etc., summing the products, and dividing by 100. The lowest possible value, if the browse were all first choice food, would be 1.00; while the highest, if it were all fourth choice or starvation food, would be 4.00.

Through use of the above two indices it is possible to arrange stands in order of browse condition and browse quality. The two indices are essentially independent, since one is based on estimated browse damage and the other on an independently derived preference rating, and it is theoretically possible to have a complete range of values of one index for any given value of the other. To give a more concise means of comparison the two were multiplied together to give an index called the pressure index. Damage to fourth choice browse species was considered to be more indicative of heavy pressure than damage to first choice species. Thus a lightly used stand of fourth choice (starvation) foods would have a value of 4.00, while a stand of first choice foods would need to be totally browsed to give the same value. The mini-

TABLE 1.—PREFERENCE RATINGS OF BROWSE SPECIES FOUND IN THE APOSTLE ISLANDS. CHOICES ARE ACCORDING TO DAHLBERG AND GUETTINGER (1956), EXCEPT THOSE NOTED WITH AN ASTERISK, WHICH WERE RATED BY THEIR CONDITION IN THIS STUDY.

1ST CHOICE	3RD CHOICE
Red Maple (*Acer rubrum*)	Balsam Fir (*Abies balsamea*)
Mountain Ash (*Sorbus americana*)	Sugar Maple (*Acer saccharum*)
Yew (*Taxus canadensis*)	White Birch (*Betula papyrifera*)
White Cedar (*Thuja occidentalis*)	Beaked Hazel (*Corylus cornuta*)
Hemlock (*Tsuga canadensis*)	White Ash (*Fraxinus americana*)
2ND CHOICE	Hairy Honeysuckle (*Lonicera hirsuta*)*
Mountain Maple (*Acer spicatum*)	Red Oak (*Quercus borealis*)
Juneberry (*Amelanchier* spp.)	Trembling Aspen (*Populus tremuloides*)
Yellow Birch (*Betula lutea*)	Large Pussy Willow (*Salix discolor*)*
Redroot (*Ceanothus ovatus*)*	**4TH CHOICE**
Round-leaved Dogwood (*Cornus rugosa*)*	Speckled Alder (*Alnus rugosa*)
Fly Honeysuckle (*Lonicera canadensis*)	Japanese Barberry (*Berberis Thunbergii*)*
Black Currant (*Ribes hudsonianum*)*	Common Juniper (*Juniperis communis*)*
Red-berried Elder (*Sambucus pubens*)	Ironwood (*Ostrya virginiana*)
Basswood (*Tilia americana*)	
Downy Arrow-wood (*Viburnum Rafinesquianum*)*	

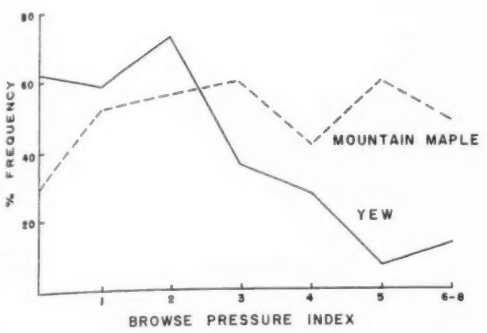

FIG. 2. The frequency of two common shrubs in relation to the browse-pressure gradient. The frequencies are averages for the stands in each of seven segments of the gradient, excluding stands dominated by pines.

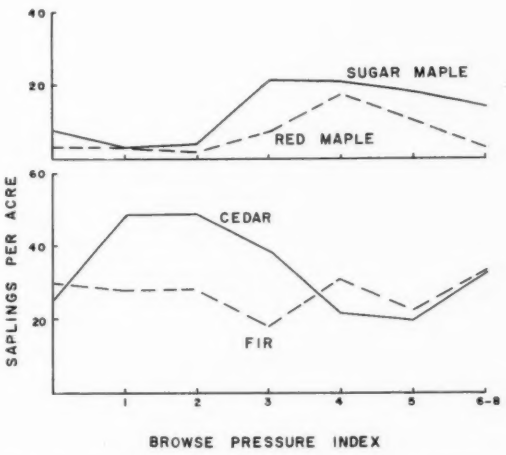

FIG. 3. The density of saplings of four common tree species in relation to the browse-pressure gradient. Densities are the average for the stand in each of seven segments of the gradient.

mum value for the pressure index is zero, for any stand that has not been browsed regardless of the preference rating of the species it contains. The theoretical maximum value would be 16, for stands containing all fourth choice food, all totally browsed. The maximum value actually obtained was less than 8, and it is unlikely that a value near 16 could ever be reached under natural conditions, since deer would die before they had reduced a stand composed entirely of fourth choice foods to the totally browsed condition.

RESULTS

The results of this investigation may be grouped into two categories: the effect of deer on individual species and the effect of deer on the vegetation considered as a unit. Figures 2 and 3 show the effect of deer, as measured by the pressure index, on several important browse species. The stands have been arranged in order of increasing pressure. In Fig. 2, the measure of the species is frequency, the percentage of quadrats in each stand in which the species occurred. It can be seen that the frequency of yew tended to decrease as the pressure index increased, while mountain maple appeared to remain fairly constant, showing, if anything, a slight increase as pressure on browse increased. In Fig. 3, the species data are saplings per acre. Balsam

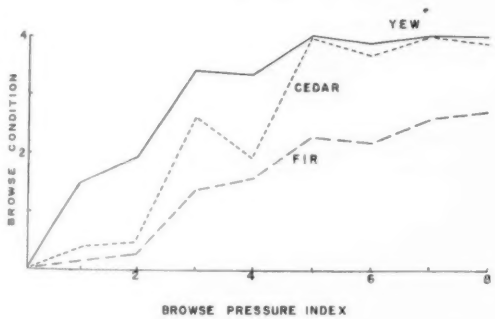

FIG. 4. The relation of browse damage on three coniferous species to the browse pressure of the stands. Browse condition values were averaged for the stands in each of nine segments of the pressure gradient.

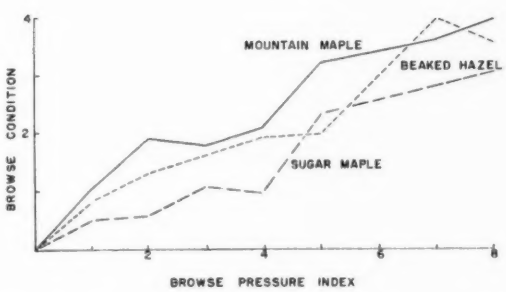

FIG. 5. The relation of browse damage on three deciduous species to the browse pressure of the stands. Browse condition values were averaged for the stands in each of nine segments of the pressure gradient.

fir showed no definite trend, but the other three species did show distinct differences. White cedar saplings were most numerous in stands with a low pressure index, while the quantity of sugar maple and red maple saplings tended to reach a peak in moderately and heavily browsed stands. All these species except balsam fir showed a decrease at the heavily browsed end of the figure.

Several important species not graphed had a pattern of this pressure-on-browse gradient similar to that of balsam fir. They include white and yellow birch saplings, and beaked hazel (*Corylus cornuta*).

Figures 4 and 5 show the condition of browse plotted against the pressure index. The fact that condition of browse is one of the components of the pressure index means that the two axes are not completely independent. However, the pressure index is calculated by multiplying the average condition of all browse stems by the average preference value of these stems for any stand, and browse condition values for indi-

TABLE 2.—BROWSE DATA FOR STANDS ARRANGED ACCORDING TO THE LEADING TREE DOMINANTS

	No Pressure	Light Pressure	Moderate Pressure	Heavy Pressure	Very Heavy Pressure
YELLOW BIRCH-WHITE CEDAR					
Number of stands	4	7	3	21	2
Min. browse per acre	22,000	1,500	900	600	300
Browse cond.	0.00	0.87	1.86	3.51	3.09
Preference	1.11	1.52	1.45	1.63	2.19
WHITE CEDAR-BALSAM FIR					
Number of stands	1	3	2	3	3
Min. browse per acre	11,000	800	400	400	200
Browse cond.	0.00	0.85	1.77	2.48	2.96
Preference	1.06	1.75	1.45	2.12	2.33
SUGAR MAPLE-YELLOW BIRCH					
Number of stands	4		4	2	2
Min. browse per acre	1,300		300	36,000	100
Browse cond.	0.00		1.68	1.80	3.02
Preference	1.64		2.15	2.84	2.28
YELLOW BIRCH-HEMLOCK					
Number of stands	6			2	
Min. browse per acre	2,100			600	
Browse cond.	0.00			2.43	
Preference	1.47			2.09	
RED OAK					
Number of stands			2	2	
Min. browse per acre			12,000	500	
Browse cond.			1.21	2.04	
Preference			2.72	2.60	
PINE					
Number of stands	1	1		1	2
Min. browse per acre	300	20		1,600	1,000
Browse cond.	0.00	0.15		1.68	2.39
Preference	2.64	2.73		2.46	2.61
ASPEN					
Number of stands	1	1	2	4	
Min. browse per acre	1,300	1,000	700	500	
Browse cond.	0.00	0.48	1.32	1.82	
Preference	2.26	2.84	2.46	2.74	

vidual species in the stand may be quite different from the average condition value. The three coniferous species plotted in Fig. 4 showed quite different patterns. Yew was apparently the preferred food and decreased rapidly as browse pressure increased. White cedar remained relatively undamaged until yew reached the moderately damaged condition, and then showed a very rapid increase. Balsam fir was eaten only after the two more preferred species were in poor condition.

Three deciduous browse species are plotted in Fig. 5. There was a distinct trend toward increased damage as the pressure index increased, but the pattern is quite different from that of yew and white cedar. The abrupt rise characteristic of the curves of the two coniferous species is not apparent, and the curves are more nearly straight.

The effect of deer on the vegetation is summarized in Tables 2 and 3. Table 2 has the stands arranged according to the dominant tree species in the stand, with a further subdivision based on the pressure-on-browse index. Five categories of browse pressure were used, based on the following index values: 0—none, .01–2.00—light, 2.01–4.00—moderate, 4.01–6.00—heavy, 6.01 and over—very heavy. The number of stems as measured by the minimum density dropped as the pressure index increased. The preference rating of the stands also deteriorated as pressure increased. Of the stands with no pressure, yellow birch-white cedar stands and white cedar-balsam fir stands had the greatest density of browse stems, and these browse stems were of a higher quality than those of other communities. Perhaps red oak stands also have provided excellent habitat, but since there were no oak stands on islands without deer, no direct comparison could be made. In those stands where pressure had reached the moderate category, differences between communities became less distinct. Most stands showed a marked decrease in minimum density and a rise in the preference index of the browse, with two exceptions. The moderately browsed oak stands had a high minimum density but were apparently not good deer habitat, judging from the preference rating of the browse in these stands. The two heavily browsed sugar maple-yellow birch stands should perhaps be placed in a separate category, since they had only one important dominant, sugar maple. They were selectively cut Oak Island stands which had been red oak-sugar maple stands prior to cutting. The high minimum density was

TABLE 3.—BROWSE DATA AVERAGED BY ISLAND

Island	No. of Stands	Minimum Browse Per Acre	Condition	Preference	Pressure
Rocky	6	200	3.04	2.10	6.42
Stockton	6	600	2.76	2.19	6.04
Basswood	1	200	2.26	2.44	5.52
Madeline	4	600	1.98	2.62	5.19
Hermit	3	200	1.67	2.73	4.64
Oak	9	7,000	1.65	2.67	4.12
South Twin	2	1,300	1.90	1.89	3.54
Bear	3	700	2.02	1.47	2.92
Manitou	2	500	1.56	1.56	2.49
Michigan	6	2,000	1.00	1.81	1.66
Otter	3	600	0.79	1.69	1.58
Cat	4	3,100	0.91	1.46	1.33
Sand	2	2,000	0.00	1.64	0.00
Outer	12	2,900	0.00	1.56	0.00
Devils	2	9,000	0.00	1.32	0.00
Raspberry	1	270,000	0.00	1.25	0.00
York	1	11,500	0.00	1.06	0.00
North Twin	1	10,900	0.00	1.00	0.00

probably due to the open canopy. In browse condition and preference they were more similar to the red oak stands than to the sugar maple-yellow birch stands with which they have been placed.

Table 3 presents the data for the same stands arranged according to the island on which the stands were located, in the order of increasing pressure index.

DISCUSSION

In a study of the effect of deer on vegetation it would be ideal to examine two elements of the deer browse factor—the intensity of browsing and the length of time that browsing has occurred (at a known intensity). In this project no way of quantitatively measuring the second element was possible, so that the results of this study are based primarily on the relation between present browse intensity and the present vegetation. The history of deer herds on the individual islands is not completely known. Annual surveys on the ground and from the air have been made for the past 4 years. Hunting records (Table 4) are available, but these are very imperfect indications of deer densities, since islands vary in their accessibility and accommodations.

The history of the vegetational disturbance is also imperfectly known. All the islands except Devils and North Twin, and small portions of some of the other islands owned by the federal government, have been logged. They all were subjected to considerable disturbance during the period when steamship travel was the common mode of transportation in this region. Within the last five years Ironwood has been heavily logged, Otter has been logged to a lesser degree, and remaining virgin stands on Outer Island are being cut at the present time.

When the stands are arranged along the browse-pressure gradient, deer damage to various browse species follow interesting trends. Figure 4 shows the three most common evergreen browse species. It is apparent that yew was preferred over the other two species, and until yew reached the moderately browsed condition, there was very little damage to white cedar and fir. As yew disappeared the deer seemed to feed upon white cedar with much greater intensity than before, with a resulting sharp increase in browse damage along the pressure gradient. This behavior was at least in part a function of the size of the deer herd. When the herd was small, evergreen browse used by the deer was almost exclusively yew. As the herd built up yew disappeared, and white cedar was then browsed very inten-

TABLE 4.—DEER KILL PER SQUARE MILE

Island	Area Sq. Mi.	1954		1955		1956		1957		1958	
		Gun	Bow	Gun	Bow	Gun	Bow	Gun	Bow	Gun	Bow
Basswood	3.1	8.4	0.6	4.2	–	8.4	–	5.2	–	3.2	–
Bear	3.8	13.9	0.4	13.6	0.4	10.0	–	11.1	–	9.3	–
Cat	1.5	–	–	–	–	–	–	–	–	0.9	–
Hermit	1.0	13.3	1.3	8.7	–	6.7	–	7.3	–	1.3	–
Ironwood	2.5	5.0	–	1.0	–	8.0	–	6.0	–	4.0	–
Madeline*	22.0	1.9	0.1	3.5	–	3.7	0.1	4.4	0.3	2.7	0.2
Manitou	2.5	16.4	–	15.2	–	3.2	–	4.8	–	5.2	–
Michigan	3.0	0.3	–	–	–	1.7	–	–	–	0.3	–
Oak	8.0	1.1	–	1.2	–	1.4	–	0.8	–	0.6	–
Otter	2.6	1.2	–	2.7	–	3.1	–	3.1	–	2.3	–
Rocky	2.0	20.0	41.0	15.0	14.0	22.5	4.5	3.0	–	11.0	–
South Twin	0.8	1.2	–	1.2	–	12.5	–	16.2	2.5	2.5	–
Stockton	16.5	7.8	0.1	4.5	–	3.0	–	0.7	–	0.1	–
Avg. per. sq. mi. on islands with deer		5.2	1.4	4.4	0.4	4.3	0.2	3.2	0.1	2.3	0.1

* Madeline regulations same as mainland— buck only; all other islands are any-deer.

sively. Fir never reached the degree of damage found on the other two species. The browsing of deciduous species was quite different. The three species plotted in Fig. 5 showed an almost linear rise in browse damage as the pressure on the stand increased, although the rate of rise was somewhat different. It would appear that deciduous browse was taken independently of the kind of evergreen browse present, and that even with an abundance of the highly preferred yew, the deer still ate a fair proportion of deciduous browse. At one point beaked hazel and sugar maple, both considered third choice foods, were more browsed than white cedar, which is considered first choice.

Figure 6 shows more clearly this relation between deciduous and coniferous browse. With increased frequency of yew, damage to cedar browse dropped off rapidly, while on the other hand damage to mountain maple dropped but slightly. The question arose whether the preference for deciduous and coniferous species can be put on the same scale. The authors, utilizing the information on the browse condition of each species, ordered the species according to their relative damage. The following order resulted: yew, mountain maple, red maple, white birch, beaked hazel, white cedar, fir, sugar maple. Many deciduous species suffered greater damage than coniferous species listed as first choice food by Dahlberg and Guettinger (1956). Because the order derived from the data of this study did not take into account differences in choice due to densities of other species, composition of adjacent stands, etc., an order based on actual observation and on much more field experience was considered a more reliable guide. Therefore, the listing of the Wisconsin Conservation Department (Dahlberg and Guettinger, 1956) was used to calculate the preference rating.

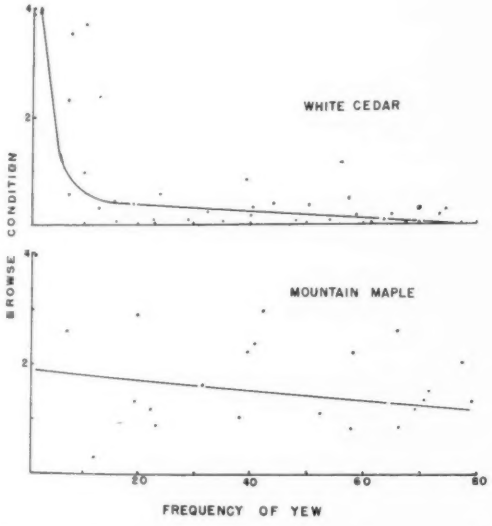

FIG. 6. The relation of frequency of yew to the browse damage of two other species. Each dot represents a stand with a browse-pressure index value greater than 1.00 and with at least 10 percent frequency of cedar or mountain maple respectively.

The typical, mature vegetation of the Apostle Islands, with yellow birch and/or white cedar among the dominant trees, is a rich source of deer food. When undisturbed, its understory is composed largely of yew, but when deer are able to utilize this food, the yew rapidly disappears (Fig. 4), and under heavy deer damage white cedar also tends to decrease (Fig. 3). Deciduous browse tends to increase in relative density under light or moderate browse pressure, as shown by the three species of maples in Figs. 3 and 4. This can be attributed to the greater sprouting ability of these deciduous species. Thus palatable species of conifers are most severely diminished under light to moderate browsing. The deciduous browse species decline under very intense browsing.

Pine forests, which are rare on the islands, are much less valuable for deer. Because these pine stands usually have browse composed of various deciduous species of high sprouting ability compared to the conifers, such as honeysuckles (*Lonicera* spp.), and juneberries (*Amelanchier* spp.), the stands apparently do not suffer as much under browse pressure as do stands of yellow birch and white cedar. However, the apparent increase in minimum browse as browse pressure increases, as shown in Table 2, is probably due to the vegetational variability between pine stands, especially density of

trees per acre, rather than to the effect of deer. Aspen forests are also less valuable for deer and less sensitive to browse pressure (Table 2).

Analysis of the data by island (Table 3) presents several problems. An attempt was made in this study to sample the complete range of habitats that were present, and no attempt was made to make the number of stands in any one vegetation type proportional to the total area of that type. Consequently several stands were studied that represent a very small fraction of the total vegetation; this was especially true of some of the pine stands. Several islands had on their leeward sides well developed sandbars which were sometimes occupied by stands of red or jack pine. Since they were atypical of the vegetation of the islands as a whole, they were not included in the island averages. Two stands were excluded for this reason, one on Stockton and one on Outer Island. A stand on South Twin was excluded because of a very low production of browse atypical of the island as a whole. Available browse was also less palatable in this stand, and deer did not enter it, so that those browse stems that were available had good browse condition. One other stand, a conifer swamp on Devils Island, was excluded for similar reasons. Stands of this type are not deer habitat in Wisconsin (Christenson, 1954), and their inclusion would likely result in fallacious averages.

The six islands listed at the bottom of Table 3 are those without deer. As a group they had more browse stems than the other islands, and this browse was of a higher quality, as indicated by the preference index. One of them, North Twin, had nothing but first choice food in the stand sampled. The table as a whole indicates that a general correlation between the browse condition and browse preference indices existed. As conditions became poorer, the browse that remained was of the less desirable species, but in the top five islands this trend was reversed. The very poor condition of the first three islands was probably due to the presence of some first choice browse. The deer apparently could not sustain themselves when only poorer classes of food were present and consequently islands with very high preference indices (low quality food) had less damage to the browse that was present than did those islands where some choice food still existed.

In Table 3 there are five islands of similar size and topography which have quite different histories in regard to deer herds; all were small and low, with no evidence of recent cutting. Devils Island, with at least 9,000 stems of browse per acre, most of which were first choice deer food, represented the condition of islands without deer. On Cat Island the deer herd had not reached sufficient size to affect species composition materially, although density of browse had decreased.

South Twin, at the time the stands were sampled (1956), still had abundant yew, but most of it was in the moderately browsed category. Physical evidence of a large herd was present—well developed trails and numerous droppings. Evidence indicated the deer were still increasing. Rocky Island reached a population peak in 1954, and at the time of sampling appeared to be in the worst condition of any island. Hermit suffered an irruption some time prior to 1954, and the herd had effectively removed most of the highly preferred browse (Waskow and Curran 1954). Browse conditions appeared to have improved, but this was due to the absence of recent large-scale deer activity—there was little left for deer to eat.

The data indicate that the lightest deer pressure on these islands will result in some vegetational change. Whether or not an equilibrium could be established that would preserve the high food quality and density of browse on deerless islands, and still support a deer herd, is very questionable. Yew is apparently a highly nutritious food as well as a highly preferred one, judging from the rapid build-up of deer herds on some of the islands. It seems to be very sensitive to browse damage, however, and rapidly disappears even under moderate browsing. This combination of high palatability and low resistance to browsing makes it an in-

efficient deer food, and it is probable that under the vegetational conditions existing on the Apostle Islands (and very likely throughout most of the northern lake states) deer and yew are incompatible.

Distribution of deer on the islands is not based on food supply alone nor on the proximity of the islands to the mainland or to each other, since some islands with ample food, close to the mainland, are not inhabited. Cover requirements and needs for openings may limit the distribution. As more cutting and clearing are taking place, however, deer are apparently invading new islands. Some vegetation of unbrowsed islands is probably similar to that of the original forest in northwest Wisconsin. Because of the interesting historical and botanical nature of this vegetation, some of it should be preserved from deterioration by man or deer. Deer might be kept from the islands when certain habitat requirements, such as openings, are lacking. Where deer already occur or are desired, some kind of management, such as intensive hunting and/or limitation of openings, should be undertaken. Otherwise on islands with excellent food supply deer will multiply until they have starved themselves and drastically reduced the carrying capacity of the range.

ACKNOWLEDGMENTS

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SUMMARY

Seventy-six stands of forest vegetation on the Apostle Islands were sampled for browse stems by the point-centered quarter method. Damage to the browse by deer was also recorded. The stands represented a number of vegetation types, including pine, aspen, oak, hemlock, sugar maple, and yellow birch-white cedar forests. The last-mentioned type predominated in the region. Indices were prepared for browse pressure, based on damage, palatability of browse, and density of browse. Cedar saplings and yew tend to decrease in density with increased browse pressure, while mountain maple tends to increase. Yew was preferred by deer to any other coniferous food. Deciduous foods such as mountain maple are an important part of the cervine diet, and these may be much more heavily browsed than cedar if yew is plentiful enough to provide sufficient coniferous food. The best habitat for deer appears to be the unbrowsed yellow birch-white cedar stands. When these stands are subjected to moderate or heavy browsing, however, their food value diminishes rapidly.

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NATURAL MORTALITY PATTERNS OF DEER IN SOUTHEAST ALASKA[1]

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Knowledge of population-regulating factors such as birth rate and mortality is of obvious importance in the study of animal populations. The task of securing this information is in many cases perplexingly difficult. Fortunately, in Southeast Alaska the unique association of the black-tailed deer (*Odocoileus hemionus sitkensis*) with its range affords an exceptional opportunity for the collection of natural mortality information. During some winters adverse climatic conditions, coupled with the abrupt mountainous topography, force the deer to utilize a narrow fringe of range adjacent to the beaches where snow depth is at a minimum. Natural mortality is greatest during this critical winter period, resulting in the accumulation of deer carcasses in areas where they can be readily found. This paper deals with the sex and age characteristics and the causes of natural mortality in black-tailed deer populations under Alaskan conditions.

The period of study (1952–1956) was concurrent with an increasing deer population. From a population low in 1949, following several years of excessive winter losses, deer increased to the point of overpopulation in some areas by 1956. Harvest data and browse utilization studies in 1955 and 1956 indicated several over-stocked ranges, and associated range deterioration was evident in some winter concentration areas. However, Southeast Alaska is a complex and much divided geographical unit (Fig. 1), and incongruity of conditions frequently is the rule rather than the exception. In the extreme southern region, for example, low deer population levels were in contrast regions and apparently represented a slower to high densities in central and northern rate of recovery from the low of 1949.

The wolf (*Canis lupus*) is the only significant natural predator of deer in Southeast Alaska and is restricted in distribution to the islands southeast of Frederick Sound and the mainland. A limited wolf control program was in operation during the course of the study. While it is not possible to eval-

[1] In Southeast Alaska quantitative deer winter mortality studies were begun in 1952 by the Fish and Wildlife Service through funds derived from Federal Aid in Wildlife Restoration Project W-3-R. The work was done in 1952, 1953 and 1954 by Olson and in 1955 and 1956 by Klein.

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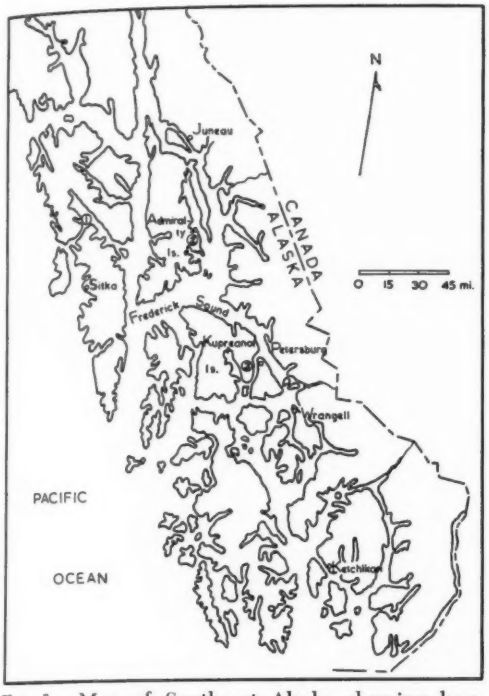

FIG. 1. Map of Southeast Alaska showing locations mentioned in the text. Areas numbered are, (1) Peril Straits, (2) Mole Harbor and (3) Wrangell Narrows. Area covered by map corresponds quite closely with the native range of deer in Alaska.

uate the effectiveness of the control program, wolves were common throughout most ranges southeast of Frederick Sound during this time. Notwithstanding local exceptions, removal of wolves by control measures may have created merely a temporary reduction in population, and may not have inhibited the annual increase.

A 3-month open season with a limit of two bucks was in effect during 1952 and 1953. In 1954 the limit was increased to three, and a limited doe season was initiated for the first time in 1955. Winters were relatively mild during the period of the study, with the exception of 1955–56, which was characterized by a cold, snow-free, early winter with excessive but localized snow accumulation during the late winter.

METHODS

The method of study was essentially a spring reconnaissance of important deer wintering areas in Southeast Alaska. Sample segments of the range were chosen in each area and a thorough search made for the remains of dead deer. Early studies revealed that 90 percent of the deer dying as a result of winter starvation were found within 100 feet of the beach. On this basis, we designated 100-foot-wide strips of range adjacent to the beach as index areas at each winter concentration area checked. In most instances, carcasses found were reduced to skeletons and fragments of hide by carrion-eating birds and mammals. The remains were sexed by examination of secondary sex characteristics of the skull or pelvis and aged by the tooth replacement and erosion method. The condition of the bone marrow of the femur or humerus was used as a criterion of physical condition of the deer at the time of death (Cheatum, 1949). Deer with red or pink, watery-gelatinous, bone marrow were considered to have died either directly from starvation or indirectly as a result of malnutrition. Carcasses found with fat reserves remaining in the bone marrow were considered deaths from causes other than starvation, such as accidents and predation. Frequently location or condition of the kill would indicate the actual cause of these "other" deaths.

Practical limitations prevented complete coverage of all deer-wintering areas throughout Southeast Alaska. Consequently, the study was restricted to those areas readily accessible to hunters and supporting the major hunting pressure.

FINDINGS AND DISCUSSION

Causes of Mortality

Starvation accounted for the greater part of winter mortality. Deaths from predation and accidents, including drowning and falls, did not exceed 20 percent of the total winter mortality during the study. Table 1 shows the ratios of deaths from starvation to those from other causes. It is less likely that deaths from causes other than starvation would be confined to the narrow wintering range adjacent to the beach; consequently, the frequency of occurrence of such deaths may be somewhat greater than is indicated

TABLE 1.—RATIOS OF DEER DEATHS FROM STARVATION TO THOSE FROM OTHER CAUSES IN SOUTHEAST ALASKA

Year	Deaths per Mile of Beach		Deaths from Other Causes, Percent of Total Kill
	Starvation	Other Causes	
1952	0.9	0.2	18.2
1953[1]	–	0.1	–
1954	0.6	0.1	14.3
1055	1.0	0.3	23.1
1956	2.3	0.4	14.8

[1] Starvation losses were negligible.

TABLE 2.—WINTER DEER LOSSES IN SOUTHEAST ALASKA 1952, 1954, 1955 AND 1956

Area	Number of Dead Deer Found per Mile of Beach Checked[1]			
	1952	1954	1955	1956
PETERSBURG-WRANGELL	0.6	0.1	0.6	1.7
Wrangell Narrows			0	2.0
SOUTHERN ADMIRALTY IS.	1.5	0.7	0.8	2.4
Pybus Bay			0.5	0.7
Gambier Bay			0.6	1.7
Mole Harbor			0.7	3.3
SITKA-PERIL STRAIT		1.5	1.5	4.7
Nakwasina Passage			2.5	12.0
Deadman Reach			4.0	10.0

[1] Values based on approximately 15 linear miles of beach fringe surveyed annually on all areas.

in the data presented. The increase in numbers of "deaths from other causes" found per mile of beach after 1954 is to be expected with an increase in total population. The rate, however, probably did not change and within certain population and environmental limits, it is logical to assume that the death rate from accidents and predation remains constant and does not fluctuate with the population level. Excessive over-population, with correspondingly increased activity from crowding, undoubtedly would result in an increased mortality rate from causes other than starvation.

Regional Variations of the Mortality

The extent of winter losses of deer in Southeast Alaska is determined by many variables, of which range condition, population numbers and weather are perhaps the most important. This is borne out by regional comparisons of winter mortality, shown in Table 2.

In the central Petersburg-Wrangell area, rapidly increasing deer herds have resulted in heavily stocked ranges, but browse conditions are still relatively good. Evidence of deterioration of winter range from overbrowsing by deer has become apparent in the past two years, but carrying capacity has not been greatly reduced. Winter mortality has not been heavy in spite of the large number of deer. The heavy snows during the winter of 1955–56 resulted in slight increases in mortality rates in the Petersburg-Wrangell area. Although snow depth exceeded 5 feet in some areas, the snow-free early winter and the short duration of excessive snow depths occurring in March resulted in a minimal critical period. However, if the population trend continues in these areas, it is inevitable that increasing losses will occur in the future under the adverse effects of over-population on the range.

Large deer populations on southern Admiralty Island did not suffer heavy winter mortality during the years of the study. Bays on the south end of the island, exposed to the warm flow of air accompanying frequent southeasterly storms, did not accumulate the deep snows common to other areas; consequently, during the winter of 1955–56 mortality was not significantly increased over the previous years. Mole Harbor, however, showed an increased mortality rate in 1956. This area lies about 20 miles north of the other southern Admiralty Island areas and is exposed to the colder effects of northerly winds blowing down Seymour Canal. Range conditions are similar in these Admiralty Island areas; thus the greater snow accumulation in the Mole Harbor area apparently accounted for the larger kill there.

In the Sitka-Peril Strait area several years of continued high deer populations seriously reduced the carrying capacity of the winter range. Winter losses have been correspondingly greater than in other Southeast Alaska areas. In the winter of 1955–56 snow conditions were comparable to those in the Petersburg-Wrangell area, with average late

winter depths of 4–5 feet. The 1956 loss of deer averaged 4.7 deer per mile, which is considerably higher than other Southeast Alaska areas with similar winter conditions. At Deadman Reach and Nakwasina Passage losses of 10 and 12 deer per mile are extreme examples of the results of over-stocked conditions existing in the Sitka-Peril Straight area.

Yearly and regional variations in winter mortality can frequently be attributed directly to browse abundance and availability, and depth and duration of snow, but other factors may be of importance in determining the kill. On marginal ranges, browse quality may be equally as important as quantity and availability; also, the frequency of occurrence and nutritive value of secondary browse species may be of considerable significance (Cowan and Wood, 1955; Einarsen, 1946; French, *et al.*, 1955). Summer and fall range quality is important in determining the condition of deer going into the winter (Robinson, 1956). All these factors are related to deer survival; however, the condition that triggers excessive winter losses usually is over-stocking of winter range. This is wasteful of deer and destructive of range as well. A comparison of weather, population pressures, and range conditions with deer losses during severe winters for various areas in Southeast Alaska leads to the following conclusions: (1) on properly stocked ranges in good condition, losses are tempered by favorable browse conditions; (2) fawns represent almost the entire mortality on the better ranges, *e.g.*, 84 percent in the Petersburg-Wrangell area in 1956; (3) conversely, on over-stocked depleted ranges, losses are excessive and mortality is characterized by a large proportion of over-age deer.

In the Sitka-Peril Strait area in 1956, fawns accounted for only 40 percent of the losses as compared to 50 percent for deer over 5 years of age. Age differences in mortality occurring between the areas of, (1) good range conditions and adequate stocking and (2) severely deteriorated and over-stocked range, are understandable if age structures of the two populations are examined. Hunter-harvest data for 1956 show that deer on good range in the Petersburg-Wrangell area are rapidly increasing, with a large proportion of young deer in the population. Deer 1½ and 2½ years old made up 54 percent and deer over 5 years of age comprised less than 2 percent of the hunter-kill. Similar data from the over-stocked ranges in the Sitka-Peril Strait area indicate a more stable deer population with young deer, 1½ and 2½ years old, representing only 16 percent of the harvest, while old deer over 5 years of age accounted for 23 percent of the 1956 hunter-harvest. Variation in the age structure of winter-killed deer offers a general criterion for the evaluation of the dynamics of population growth and has proved an asset to deer studies in Alaska, particularly in areas where hunter-harvest information is not obtainable.

Age Characteristics of the Mortality

In Alaska, winter losses of deer from starvation exhibit characteristic patterns of sex and age mortality. Mortality rates are highest among the fawn and old age groups, whereas 1½- to 5-year-old-deer, the prime age groups, usually account for less than 10 percent of the total loss from starvation. Table 3 shows that this relationship has remained relatively constant for several years.

Under Alaskan conditions, five years appears to be the upper limit of physiological efficiency in deer. Excessive erosion of the teeth and other age-incurred debilitating factors result in a reduced ability of over-age deer to survive the critical winter period; consequently, a high percentage of old deer is represented in the kill.

The age distribution of the kill appears logical upon examination of the food economy of deer. Summer growth requirements of immature deer for the production of muscle and bone tissue result in a reduced accumulation of fat, while adult deer, having attained their growth, are able to convert almost all their caloric intake, above basal metabolic needs, into fat. Consequently adult deer with greater energy reserves in the form of fat are better equipped to survive the critical winter period when

TABLE 3.—SEX AND AGE RATIOS OF 323 DEER THAT DIED FROM STARVATION IN SOUTHEAST ALASKA, 1952 AND 1954–56

Age and Sex	1952		1954		1955		1956		ALL YEARS	
	No.	Percent	No.	Percent	No.	Percent	No.	Percent	No.	Percent
FAWNS										
Males	13	16	1	2	16	25	30	23	60	19
Females	16	20	9	20	18	28	28	21	71	22
Sex Unknown	31	39	8	17	3	5	8	6	50	15
TOTAL	60	75	18	39	37	58	66	50	181	56
ADULTS UNDER 5 YEARS										
Males	2	3	2	4	1	2	5	4	10	3
Females	8	10	0	0	1	2	7	5	16	5
Sex Unknown	1	1	0	0	0	0	0	0	1	0
TOTAL	11	14	2	4	2	3	12	9	27	8
ADULTS OVER 5 YEARS										
Males	6	8	4	9	2	3	5	4	17	5
Females	2	3	21	47	19	30	50	38	92	28
Sex Unknown	1	1	1	2	4	6	0	0	6	2
TOTAL	9	11	26	57	25	39	55	41	115	36

the amount and/or quality of food available to individual deer may drop below that required for basal metabolism. In addition, experience, independence, larger size and strength enable adult deer to forage for food under conditions too difficult or fatiguing for fawns.

The sequence of events leading to fawn mortality became dramatically apparent during the heavy snows of 1956. Daily observations were made on a 7-mile length of beach range on Kupreanof Island in the Wrangell Narrows area during the 3 weeks immediately following the maximum snow accumulation of 83 inches on March 7. Observations of deer on the beaches were made with the aid of binoculars from a small outboard-powered boat. Table 4 shows the gradual changes in fawn-adult ratios that were brought about by the loss of fawns during this period. Related snow depths are also shown in Table 4. Most of the snowfall occurred in 3 consecutive days, restricting deer activity through their inability to keep trails open. Much of the snow was intercepted by trees; consequently, snow depth was irregular within the timber fringe and not as great as in openings and in areas adjacent to the beach. Much of the normally available browse was covered with snow, but some taller plants which previously had been out of reach became available to the stronger and larger deer able to forage in deeper snow. In the few days before settling and packing made travel on top of the snow possible, fawns floundered helplessly, going without food except for beach kelp (*Fucus* sp.) and hemlock (*Tsuga heterophylla*), which are of low protein analysis and of doubtful nutritional value. Fawns had survived the greater part of the winter but were in poor condition prior to the deep snow. By March 9 they were so weakened that they were unable to follow the adults except

TABLE 4.—FAWN-ADULT RATIOS IN THE WRANGELL NARROWS AREA, DECEMBER–APRIL 1955–56

Date	Fawns	Adults	Fawn–Adult Ratios	Snow Depth (in.)[1]
12/15	13	27	48:100	10
2/26	12	21	57:100	18
3/1	6	13	46:100	30
3/8	9	31	29:100	70
3/10	20	56	36:100	54
3/13	22	66	33:100	46
3/16	14	28	50:100	28
3/19	4	30	13:100	23
3/20	2	24	8:100	21
3/21	16	91	17:100	19
3/23	6	43	14:100	16
4/10	5	35	14:100	12

[1] Greatest depth of 83 inches occurred on March 7, 1956.

on the more frequented trails, and some were dying from starvation. Mortality from starvation continued for the next 2 weeks until conditions were improved by rains and warmer weather. Eleven out of the 14 deer dying from starvation in this area were fawns. Observed fawn-adult ratios from beach counts of live deer changed from over 45 fawns:100 adults before the snows, to approximately 15 fawns:100 adults at the end of the critical period of 10–17 days (Table 4).

Sex Characteristics of the Mortality

The predominance of old does represented in the winter mortality is not necessarily indicative of a higher mortality rate for this segment of the population (Table 3). If an unbalanced sex ratio heavy to females exists in the population, and this appears to be the case, a larger proportion of females would be expected to be present in the kill, even though actual mortality rates were similar. However, a large proportion of bucks remain unaccounted for, if sex ratios at birth are assumed to be nearly equal. The removal of bucks by hunting cannot explain the lack of bucks in older age classes. Although hunting is an important factor in the removal of bucks in the heavily hunted areas adjacent to human populations, the outlying areas comprising most of Southeast Alaska receive only light hunting pressure. Natural mortality, therefore, is instrumental in bringing about this unbalanced sex ratio. In California, Taber and Dasmann (1954) found differential postnatal sex mortality among black-tailed deer fawns during their first winter. Longhurst and Douglas (1953), in the same state, found similar differential sex mortality among fawns occurring during summer. In both cases male fawns suffered the heavier mortality. However, studies of mule deer in Utah (Robinette, *et al.*, 1957), indicated heavier postnatal loss of male fawns during the first few months of life, but they concluded that the winter mortality rate is higher on female fawns, although some variations existed with range and weather conditions. In arriving at their conclusion, Robinette, *et al.* (1957) compared sex ratios of winter-lost fawns with sex ratios in the hunter-harvest. They assumed equal susceptibility of both male and female fawns to hunting loss.

We believe that differential sex mortality among fawns occurs under Alaskan conditions, although this is not confirmed by our studies. It seems likely that the higher metabolic rate of males resulting from a greater rate of growth, activity, curiosity and independence than occurs among females would account for a heavier postnatal mortality among male fawns (Brody, 1945). Fawn carcasses examined by us during the first 5 years of the study showed a ratio of 85 males:100 females. A possible reason for this disparity with assumed conditions lies in the method of collection of data in which mortality surveys are made in spring. Fawn carcasses are quickly removed by scavenging birds and mammals; consequently, during severe winters, remains of buck fawns dying early would be more likely destroyed or scattered before the spring surveys than carcasses from deer dying later in the winter. During the brief critical snow conditions of 1956, daily field observations allowed an opportunity to locate deer carcasses before they were lost to scavengers. Of the 11 fawn remains found during this period, 8 were males and 3 were females. In other years, while snow depths were not as great as in 1956, mortality was spread out over a longer period. Under these more moderate conditions it is quite likely that the greater independence and activity of buck fawns which would contribute to their mortality also results in their dying in more obscure locations than doe fawns.

There is some indication from studies of deer herds in other parts of North America that unbalanced sex ratios favoring females reflect poor range conditions, while on good ranges sex ratios tend to be more nearly equal. Taber and Dasmann's (1954) findings supported this thesis, and they uncovered in the literature corroborative evidence indicating that differential sex mortality accounted for the unbalanced sex ratios. There is also indication of similar differential sex mortality under Alaska conditions. Exami-

nation of old deer kills, one or more years old, made during the course of each annual survey of current winter mortality, indicated a distinct sexual variation among mortality of adults. Bucks appeared to be more susceptible to mortality during the prime ages than does. The sex ratio of 72 identified remains in the 1½- to 5-year age groups was 167 males:100 females. In older age groups over 5 years of age, the ratio was 72 males: 100 females in a sample of 127. The predominance of females in the latter sample is to be expected in light of the loss of males at an earlier age and the subsequent distorted sex ratio favoring females in the older age groups of the population. Age ratios in the hunter harvest confirm the longer life expectancy for females. In the 1956 harvest, 7 percent of the males and 22 percent of the females harvested were over 5 years of age.

Adult mortality could be materially affected by the period of occurrence of the most critical environmental conditions. Bucks undergo extreme physiological drain during the rut and recover only a small percent of their lost weight before winter conditions limit available forage (Magruder, *et al.*, 1957). Early onset of winter conditions would prevent recovery of the bucks, leaving them in extremely poor condition to enter the winter. Does, on the other hand, are in their optimum physical condition with maximum fat reserves present when winter begins. The physiological drain of the developing embryo in pregnant does is almost negligible until the final stages of gestation, and is minimal in comparison to the stresses on the doe during lactation. The doe then experiences her poorest physical condition and greatest metabolic needs at a time when forage is abundant and of high quality, while the opposite is true of bucks. In addition, the doe possesses a further survival factor; in the event that she is reduced to critical physical condition after parturition, lactation ceases and the fawn, not the doe, dies. This marked diversity between sexes in the annual metabolic cycle of adult deer very likely is an important factor contributing to greater winter mortality among males. It seems probable that the greater activity of bucks, particularly during the rut, results in a higher frequency of accidental deaths among males. Magruder, *et al.* (1957), observed that white-tailed bucks in captivity, undergoing the physiological changes of sexual maturation in August of each year, appeared more vulnerable then to disease and death than at any other time.

Predation by wolves may also be selective in removing more adult males than females, although this is not confirmed by our studies. Stenlund (1955) in Minnesota suggested that wolves showed no preference for either sex of deer. This was based on a comparison of his wolf predation data with assumed parity of sexes based on fawn sex ratios obtained from hunter harvest information. However, when his data for 63 adult wolf-killed deer, for which determination of sex was possible, are segregated, a predominance of males is apparent. Thirty-five were males and 28 females, yielding a sex ratio of 125 males:100 females. The significance of this difference is increased if the sex ratio of the existing deer population was unbalanced, with a predominance of females, and this would appear to be the case. Stenlund stated that on the wolf study area, the deer population was in excess of the desirable range capacity, hunting pressure was light or absent and starvation was the major factor causing declining numbers. Gunvalson, *et al.* (1952), in a study of Minnesota deer herds, concludes that, "In areas which have been protected from hunting for a long time and where the deer population has increased beyond the sustained carrying capacity and resulting in known starvation losses, adult does are greatly in excess of adult bucks. . . ." Therefore it seems logical to assume that does were also in excess of bucks in the northeastern Minnesota area in which Stenlund's studies were made.

Differential sex mortality among adult deer appears logical if evolutionary implications are considered. Among polygynous animals, such as deer, males take no part in the raising of young and contribute to the survival of the species only through their breeding ability. The life function of

the male is completed at the end of the rutting season, and because of their polygynous nature, the loss of a large portion of males prior to the next breeding season does not necessarily restrict productivity of the population. Females, on the other hand, do not complete their life function until their progeny have become independent. Their survival from conception through the raising of young is essential for the welfare of the species. Natural selection favors the species and not necessarily the characteristics of the individual. Natural selection would tend to perpetuate the characteristics of bucks that most actively seek out and service the does. Birch (1957) considered the significance of sex-related aspects of natural selection and stated that, "One genotype can directly affect the numbers of another sort of genotype in the same Mendelian population . . . by its greater sexual activity such as a higher mating rate or by selective mating." In the process, however, bucks with the higher mating rate debilitate themselves physiologically and lessen their chances for winter survival. Those does would be selectively favored that could survive the winter and pass on their genetic characteristics in healthy fawns. The net result of these evolutionary relationships is increased winter survival of adult females over males.

Implications of Wolf Distribution

The effects of wolf predation on deer populations in Alaska are not well documented; however, some obvious variations exist between those ranges where wolves occur and the wolf-free islands northwest of Frederick Sound (Fig. 1). Comparisons of this type are, of course, of a speculative nature. Undoubtedly, other ecological factors are involved in addition to the presence or absence of predation. The characteristics which as a general rule are unique to deer populations and ranges in those areas where wolves are absent are: stable or slowly increasing populations in excess of the winter range capacity, heavy winter mortality, and severely deteriorated winter ranges. In contrast, the typical characteristics of ranges to the southeast supporting both deer and wolves are: rapidly increasing deer populations, light winter mortality from starvation, and winter ranges in fair to good condition. The wolf-populated ranges, as a general rule, during the period of the study supported a greater annual hunter harvest of deer per unit of area under comparable hunting pressure.

SUMMARY

Deer winter mortality data collected during 1952–1956 in Southeast Alaska contained distinct patterns of sex and age distribution and regional variations in magnitude. Starvation accounted for at least 80 percent of the annual winter loss. Other causes of death were accidents and predation.

During severe winters, the following mortality patterns occur: (1) on properly stocked ranges in good condition, losses are tempered by favorable browse conditions; (2) fawns represent almost the entire mortality on the better ranges; (3) conversely, on over-stocked depleted ranges, losses are excessive and mortality is characterized by a large portion of over-age deer. Age ratios of winter-lost deer varied from 84 percent fawns on good ranges, not over-stocked, to 40 percent fawns on deteriorated over-stocked ranges.

Age-specific mortality rates are highest among the fawn and old age groups, while prime-age deer, 1½ to 5 years of age, usually account for less than 10 percent of the total loss from starvation. Five years appears to be the upper limit of physiological efficiency in deer under Alaskan conditions.

Sex variations were apparent in the mortality data only in the old age groups. The sex ratio of carcasses over 5 years of age was 18 bucks:100 does. The relative absence of old bucks in the winter loss in areas where hunter harvest of bucks is not significant is believed to be the product of heavier natural mortality of males within all age classes.

An evaluation of the general effects of wolf predation on deer populations was made by comparing aspects of deer ranges populated by wolves with ranges where wolves do not occur.

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BRIEFER ARTICLES

A TECHNIQUE FOR OBTAINING SAMPLES OF MAST

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The value of reliable estimates of mast crops has been recognized by both research and management workers for many years. Mast sampling requires either direct counts or ocular estimates of acorn numbers. The result obtained with a spotting scope is an estimate rather than an actual count, as the number of nuts on a peduncle usually can not be accurately counted. Accurately counted samples can be taken from felled trees, but logging operations seldom coincide with estimate needs.

The use of a tree pruner overcomes both of these difficulties. A technique has been developed and used in the mountains of North Carolina using a series of aluminum poles. These poles are available in 5- or 6-foot lengths and are expanded at one end so that they may be joined. A standard tree trimmer or pruner with blade and spring is attached to one pole. Plastic clothes line is used to pull the cutting blade.

A two-man crew is necessary; one man handles the pruner and the other prepares sections of the pole. With the operator standing close to the base of the tree, two or three joined poles terminating with the pruner head are pushed up, resting against a low limb or the trunk. As successive sections are added, the pole becomes somewhat flexible and support against the trunk is necessary at all times. Snap-fastenings or bolts and wingnuts are helpful to hold the upper sections together. These prevent the top section from coming off when the pruner is accidentally hooked over a wrong limb.

Trees as tall as 90 feet have been sampled. Naturally, the taller the tree, the greater the number of sections and the more unwieldy the pruner becomes. An experienced crew can obtain a sample from a tree 60 to 70 feet tall in approximately 10 minutes. In short, this method offers a means of rapid sampling which overcomes at least some of the problems inherent in ocular estimates and counts taken from felled trees.

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MOUNTAIN POCKET GOPHER FOOD HABITS IN COLORADO

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This study of the feeding habits of the mountain pocket gopher (*Thomomys talpoides*) in Colorado was made to determine by means of stomach examination the amount of above-ground vegetation consumed. Records of 285 pocket gopher stomachs on file at the Denver Wildlife Research Laboratory prompted this study. The analyses of stomachs, collected in Montana during 1932 by W. W. Smith, indicated a determined effort had been made by Kelso (1934) to separate stems and leaves from root materials. Eighty-five percent of the plant parts eaten during May, June and July were stems and leaves. Previously, above-ground parts of plants had been reported occurring only in food caches and cheek pouches of gophers.

Knowledge of the surface feeding habits of pocket gophers also may prove useful in development of better control techniques. To determine if mountain pocket gophers would take grain from the surface of the ground, aluminum-colored oat groats were scattered around fresh gopher mounds. Two to 3 days later 7 of 10 gophers trapped in their underground burrows had aluminum flakes in their stomachs which confirmed that these rodents would take food from the surface of the ground. The next step, which is the subject of this paper, was to determine the period of the year when the largest amounts of above-ground food are consumed.

Procedures

Methods used in the present analysis of pocket gopher stomachs have been described previously by Keith, *et al.* (1958). The use of histological techniques for food habits determinations was pioneered by Baumgartner and Martin (1939) and developed further by Dusi (1949).

Stomachs were collected largely from the following three areas: hay fields (mixed alfalfa and grass) near Livermore, Colorado, on the east slope of the Rocky Mountains at an elevation of 5,500 feet; an herbicide study area on Grand Mesa, Colorado, at 10,000 feet elevation; and range lands on Black Mesa, Colorado, elevation 9,500 feet, on the western slope. Collections from Livermore were

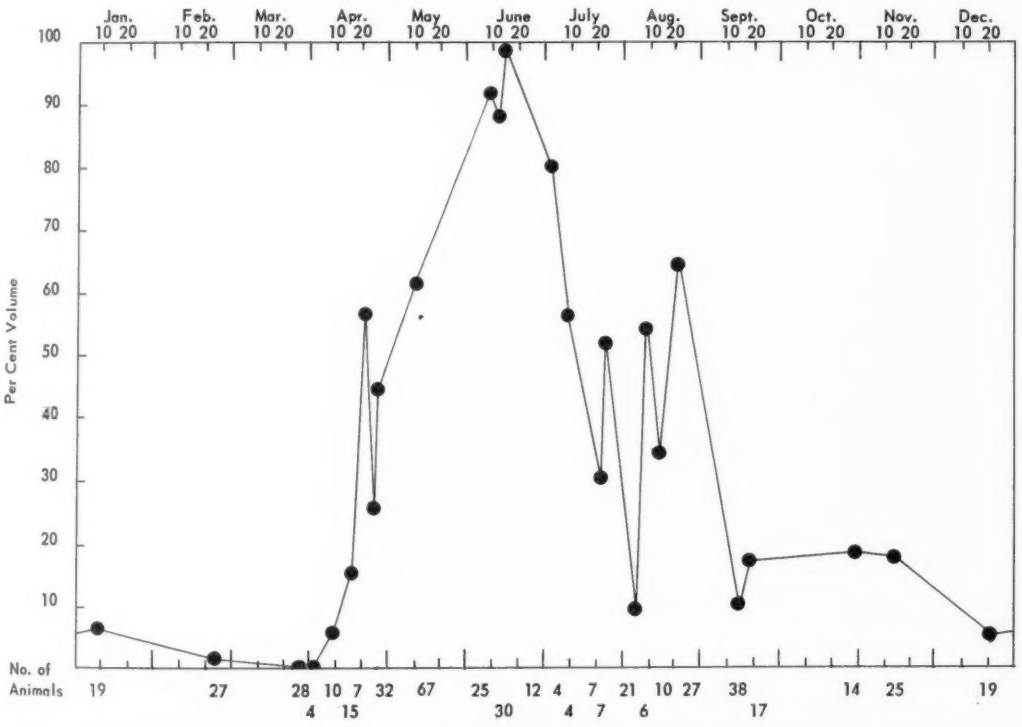

Fig. 1. The amount of above-ground vegetation in the diet of pocket gophers from Livermore, Colorado.

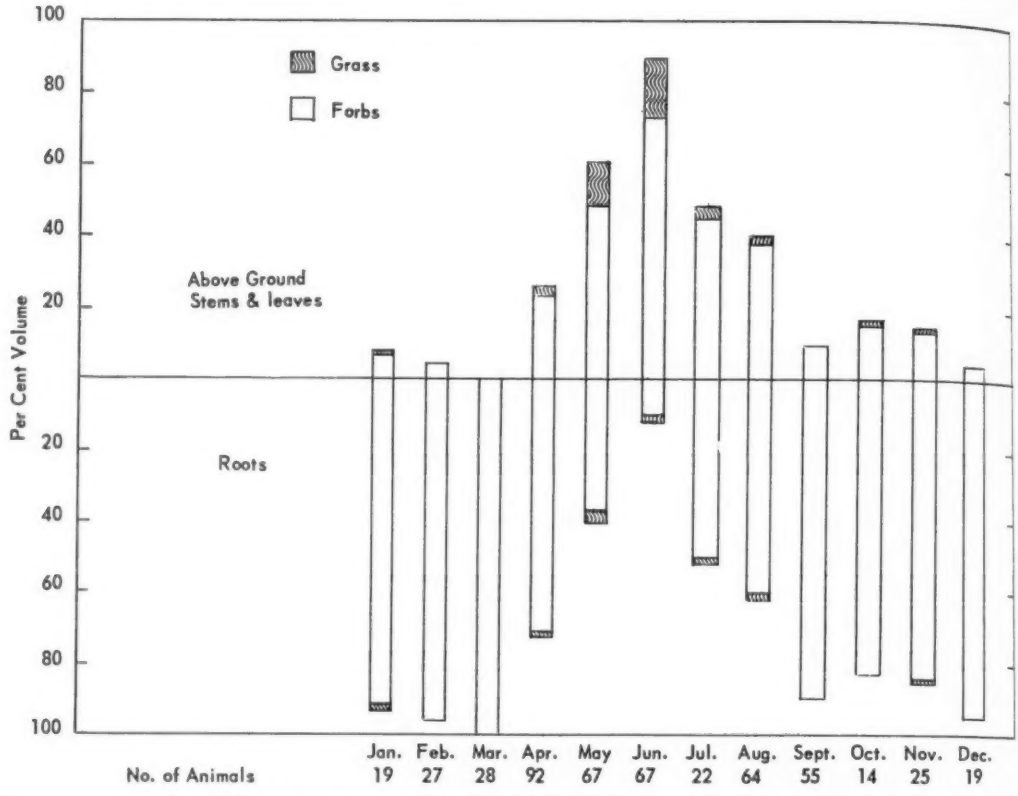

FIG. 2. The amounts of forbs and grasses and above- and below-ground plant materials consumed by pocket gophers from Livermore, Colorado.

made during all months of the year, while those from Grand Mesa and Black Mesa were made only during June, July, August, and October.

RESULTS

Figure 1 shows the relative amount of above-ground vegetation eaten by gophers living in the mixed grass and alfalfa fields near Livermore. Consumption of these plant parts was low during the winter but increased markedly in April. A peak was reached June 15 when 12 stomachs contained 98 percent above-ground vegetation. A decline occurred in July, followed by fluctuations in August that may have been due to dry weather hardening the soil to the extent that digging by gophers was affected.

Figure 2 shows the relative amounts of roots and above-ground vegetation eaten at various periods of the year, and also the amounts of grass consumed in relation to forbs (alfalfa). Grass roots did not make up more than 5 percent of the diet in any one month. Grass stems and leaves were taken in increasing amounts in April and May, with a peak of 15 percent in June, but diminished in July and August to 8.6 and 3.2 percent, respectively. The increase in consumption of stems and leaves of grasses corresponded with the increase in all categories of above-ground vegetation.

Alfalfa roots made up 96.4 percent of the diet during the December to March period. Consumption of alfalfa stems and leaves increased during April and May, reached a peak of 75.5 percent in June, and then dropped steadily through July, August and September.

Alfalfa made up 94.1 percent of the contents of the 499 pocket gopher stomachs from the Livermore area; stems and leaves amounted to 23.5 percent and roots to 70.6 percent. The picture was somewhat different with respect to grasses, with stems and leaves making up 4.4 percent and roots 1.5 percent of the gophers' diets. Throughout the year 27.9 percent of the food consumed was above-ground vegetation and 72.1 percent was root material. No animal matter was found in any of the stomachs.

Black Mesa and Grand Mesa are high altitude areas, largely inaccessible during the winter due to deep snow, and hence adequate stomach samples are available only for the June to October period. The amounts of above-ground vegetation consumed by gophers for three successive summers on Black Mesa and two summers on Grand Mesa are shown

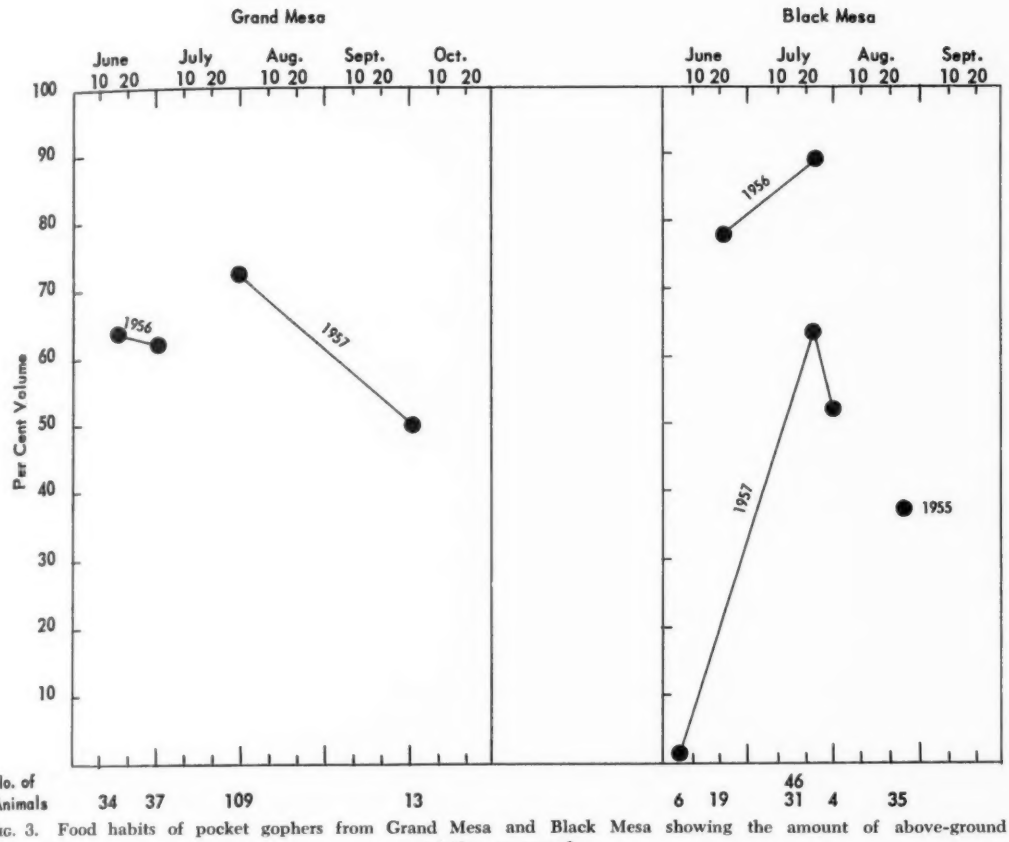

FIG. 3. Food habits of pocket gophers from Grand Mesa and Black Mesa showing the amount of above-ground vegetation consumed.

in Fig. 3. As from the Livermore area, the data from Black Mesa show that pocket gophers consume large amounts of above-ground vegetation during the summer months.

The stomachs from Grand Mesa were collected in connection with a 2,4-D herbicide study reported by Keith, *et al.* (1958). The proportion of above-ground vegetation in stomachs collected from untreated control plots in 1956 was 63.6 percent in June and 62.1 percent in July. Grass—mainly stems and leaves—constituted 28.6 percent of the diet in June and 18.9 percent in July. A sample of 109 pocket gopher stomachs taken July 31 and August 1, 1957, from the same area contained 91.9 percent forbs and 8.1 percent grass, of which 72.0 percent was above-ground vegetation and 28.0 percent was roots. By October 1 and 2, 1957, this had changed to 64.0 percent forbs and 36 percent grass, and to equal amounts of above- and below-ground vegetation.

Limited collections were made from three other areas in Colorado. Thirty-two stomachs were taken August 16, 1956, from a sheep range near Deep Lake on the White River National Forest at an elevation of 10,000 feet. These contained 91.6 percent forbs and 8.4 percent grasses; above-ground vegetation made up 75.5 percent of the contents and roots comprised 24.5 percent.

Thirteen more stomachs were taken June 19–20, 1957, from this general area but at a lower elevation. These contained 70.0 percent forbs and 30.0 percent grass; 21.6 percent was above-ground vegetation compared to 78.4 percent roots. This range, however, was still in early season development.

Eight other stomachs were collected June 21, 1957, from an improved grass pasture near Toponas, Colorado. Forbs made up 32.5 percent and grass 67.5 percent of the contents; above-ground vegetation and roots amounted to 80.0 and 20.0 percent, respectively.

REMARKS

From the results of these stomach examinations, it is apparent that much of the food of pocket gophers grows above ground. The time of year when the largest amounts of above-ground vegetation are taken depends largely on the condition of the soil and vegetation development. The soil condition, in turn, is dependent mainly on moisture or frost. In all areas where plants were still developing and not

mature or past maturity, a large amount of the stomach contents consisted of green vegetation from above the ground. It is not known how much of this vegetation might have been pulled underground to be eaten, but experiments with aluminum-coated grain showed that much of this type of food was gathered on the surface.

This information has led to field trials in surface baiting as a means of pocket gopher control. Although the results still are inconclusive, there is the possibility that under some conditions at least, surface baiting might replace the more laborious method of probing for underground burrows as a means of bait placement.

ACKNOWLEDGMENTS

The writer gratefully acknowledges the assistance rendered by co-workers of the Denver Wildlife Research Laboratory, the Agricultural Experiment Station of Colorado State University, and the Rocky Mountain Forest and Range Experiment Station of the U.S. Forest Service. Special thanks are due Evan Roberts and Sydney Tibbets of Livermore, Colorado, for permission to trap gophers on their properties.

SUMMARY

Mountain pocket gopher stomachs were collected during all months of the year from an area near Livermore, Colorado, and during the snow-free seasons, from Grand Mesa, Black Mesa, and other localities in western Colorado.

Food habits examinations disclosed that:

1. Above-ground vegetation made up a considerable part of the pocket gopher's diet during the period of the year when the plants were growing and were green and succulent.
2. Forbs were taken in preference to grasses during all periods of the year when both were plentiful.
3. Largest amounts of grass, consisting mainly of stems and leaves, were consumed during the growing season.
4. Grain baits were taken by gophers from the surface of the ground.

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A FIELD TECHNIQUE FOR ASSESSING PHYSICAL CONDITION OF SOME UNGULATES

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Several techniques for assessing the physical condition of deer in the field have been devised and applied in the management of deer populations. So far, most of these techniques have utilized deer killed either by shooting (Park and Day, 1942), or from natural causes (Cheatum, 1949). Furthermore, under special circumstances when it has been possible to obtain some measure of each sex and all age groups, the task has been time-consuming and expensive. For example, Rosen and Bischoff (1952) established norms for erythrocyte and hemoglobin counts in mule deer (*Odocoileus hemionus*), and ratings or indices to fat reserves have been used for white-tailed deer (*Odocoileus virginianus*) (Harris, 1945), and red deer (*Cervus elaphys*) (Riney, 1955). A simple field technique is needed to obtain some index to the physical condition of all sections of a population in areas where shooting is restricted to certain seasons and limited to certain sections of the population. Ideally such a technique could be applied at any time of year, to any sex or age group, and under existing game laws.

The technique here described is based on one of the many characteristics of inanition, the tendency of the animal to become thin as it drops in condition (Harris, 1945; Leopold, *et al.* 1951; Riney, 1955). Even a general estimate of the condition of a population can be valuable as one measure of response of a population to a given ecosystem (Riney, 1956).

Under most field conditions it is impossible to judge the physical condition of a deer precisely and in a way that will allow comparison with similar observations by other workers. However, sometimes populations are encountered that are in either extremely good or extremely poor condition, and

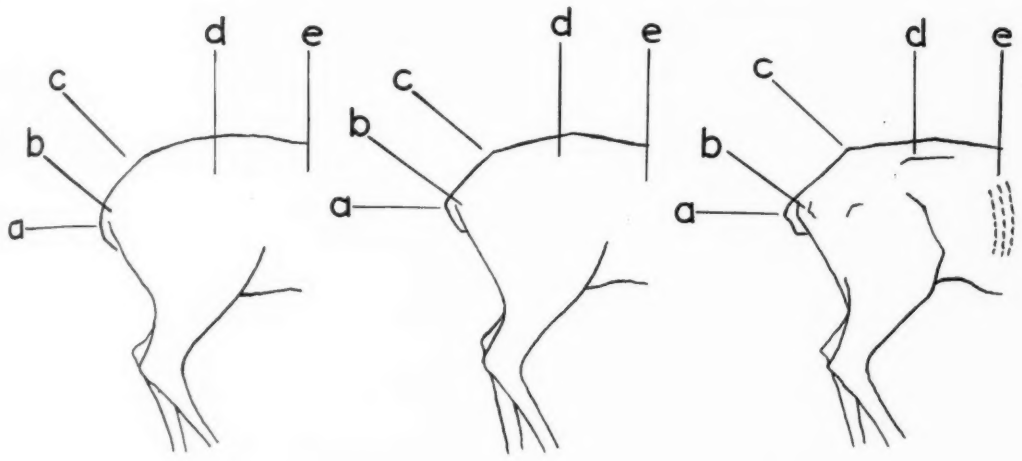

FIG. 1. General appearance of the hind quarters of deer in good, medium, or poor condition.

if sufficient care is taken, the proportion of animals of each recognizable sex and age group that fall into three general condition groups can be calculated for comparison.

As the fat reserves of the animal diminish, the tail (*a*, Fig. 1) appears more angular, the outline of a point of the pelvic girdle (*b*) can be seen, a distinct angle appears at the point indicated by (*c*), the lateral processes of the backbone vertebrae (*d*) can be seen as a faint line, and outlines of the ribs (*e*) are visible. If there are no angles corresponding to points *a* and *c* on the diagram, the deer are classed as in good condition (Fig. 1, left). If any one of the points indicated at *b*, *d*, or *e*, can be observed, the deer is classed as in poor condition (Fig. 1, right). Figure 1 (middle) represents the appearance of individuals that are not clearly in good condition or poor condition.

As with other field techniques of this type, certain arbitrary local rules will have to be followed if results are to be used for comparative purposes. For example, if red deer are observed from distances greater than 50 yards, it is necessary to use binoculars to see clearly enough to assess their condition. The maximum distance at which assessments are made will have to be determined separately for each species and in each area. A series of records should be complete, whether based on deer seen, or on deer shot, and whether for a day, a week, or a season. Sets of records can be kept either for deer observed or for deer killed; but these records should not be mixed.

This method of assessing condition is by no means as precise as the measure based on indices to fat reserves (particularly the weight of perinephric fat expressed as a percentage of the weight of the kidney) (Riney, 1955); but in New Zealand it has proved useful for many questions of management of populations where it is necessary to assess quickly conspicuous trends in condition, or for comparison of markedly different habitats. This or similar techniques can be used with but little extra time and expense if combined with other management techniques such as classification counts.

Species on which this technique has been successfully used are red deer, fallow deer (*Dama dama*), sambar (*Cervus unicolor*), feral goat (*Capra hircus*), chamois (*Rupicapra rupicapra*), and thar (*Hemitragus jemlaicus*) in New Zealand; and, in Africa, kudu (*Tragelaphus strepsiceros*), duiker (*Sylvicapra grimmia*), steenbuck (*Raphicerus campestris*), reedbuck (*Redunca arundinum*), roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*), impala (*Aepyceros melampus*), and eland (*Taurotragus oryx*). Slight modifications are being developed for several other African species whose body conformation differs enough from deer and antelope to preclude use of the same criteria, e.g., cape buffalo (*Syncerus caffer*), giraffe (*Giraffa cameloparadalis*), and blue wildebeest (*Connochaetes taurinus*).

SUMMARY

A technique is described to facilitate recording the condition of live deer and several other ungulates. Each animal classified is arbitrarily placed in one of three condition classes, good, fair, or poor, and the evidence presented as the proportion of animals in each condition class at a given locality, in a given season. Although the technique has disadvantages associated with any "rating" technique, it is inexpensive and simple to use and has proved useful in New Zealand and in Africa, especially in situations where it is impractical to kill or trap a sample of the population to assess condition.

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CONTACT DERMATITIS INCURRED FROM COTTONTAIL STOMACH CONTENTS

Gordon M. Clark, Louis N. Locke and Frederick C. Schmid

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Cottontail rabbits (*Sylvilagus floridanus mallurus*), killed during the annual December census hunt at the Patuxent Research Refuge, are routinely autopsied and searched for parasites. A severe dermatitis of the hands was incurred by one of the parasitologists as a result of examining material from the alimentary tracts of these rabbits during the 1957–58 hunt. In 1958–59 the condition was observed again in this and an additional worker. The lesions were similar to those experienced with poison ivy. Both workers were known to be highly susceptible to ivy poisoning.

In order to ascertain what part of the rabbit was the sensitizing agent, patch tests were conducted on the two sensitized workers. The inside skin of the forearm was rubbed in 1-inch squares with moist cottontail fur, muscle, heart blood and contents of stomach, small intestine and cecum of one animal. These patches were covered with moist gauze and adhesive. The subjects, within 12 hours, showed strong reaction to the contents of the stomach, cecum, and small intestine; a weak reaction to fur; and no reaction to muscle and blood. The tests suggested that the dermatitis was due to something in the ingestia of the rabbit. To verify this, stomach contents of this animal were removed, dried, and examined with a dissecting microscope. It was seen that the main identifiable bulk of the stomach contents consisted of finely ground goldenrod, lespedeza, aster, and a small identifiable trace of poison ivy. Patch tests of the dried stomach contents made at this time continued to provoke a response. Patch application of fresh, pulverized goldenrod, lespedeza, and aster failed to cause skin reaction.

Since the observed lesions on the two workers were similar to those produced by severe ivy poisoning, it seems likely that the poison ivy in the stomach contents was the cause of the dermatitis. There is no reason to suspect that digestive enzymes or larval parasites could produce these phenomena. It is probable that poison ivy is a common item of the winter diet of the cottontail in Maryland. Recurrent attacks occurred in the two susceptible individuals during handling of approximately 120 rabbits whenever tears occurred in the surgical gloves worn for protection.

It has been observed (Trippensee, 1948) that the typical winter diet of the cottontail in New England is high in bark, roots, buds, and other parts of woody perennials. In New York State poison ivy constitutes from ½ to 2 percent of the diet of the Mearns cottontail (Martin *et al*, 1951). Petrides (1942) has observed that poison ivy was "so attractive to rabbits that practically every shoot not covered by snow was consumed."

Individuals normally sensitive to poison ivy should be careful when cleaning gut-shot cottontails during the hunting season. Thorough washing with soap and water directly after handling such an animal is a helpful prophylactic procedure.

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STOMACH CONTENTS AND WEIGHTS OF SOME FLIGHTLESS ADULT PINTAILS[1]

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Information regarding natural foods of waterfowl on the Canadian prairies is confined largely to publications by Martin and Uhler (1939) and Cottam (1939). In these, food-habits data from widely separated and ecologically distinct areas of western Canada were pooled, and the great majority of stomachs apparently represented fall collections. Moreover, the sample upon which food habits within the "Western Canadian Region" were based (Martin and Uhler, 1939) included only three pintails (*Anas acuta*).

Weights of adult ducks at the flightless period of their postnuptial moult are seldom recorded in the literature.

Data presented here were obtained from ducks caught in a banding drive conducted by Ducks Unlimited (Canada) at Pel Lake, Saskatchewan, July 9, 1957. Approximately 2,000 flightless pintails, mostly drakes, were captured and banded on this occasion. The unfortunate combination of high temperatures and an unexpectedly large catch resulted in the death of about 150 birds through suffocation and trampling. These were weighed and the contents of the proventriculus and gizzard of each preserved for later examination. In addition, all "retraps" (previously banded individuals) were weighed, thereby providing a sample whose minimum age, at least, was known.

Pel Lake, a Ducks Unlimited project 65 mi. north of Regina, has a surface area of 565 A. and an average depth of around 3.5 ft. Its waters are saline. Alkali bulrush (*Scirpus paludosus*), sago pondweed (*Potamogeton pectinatus*) and hardstem bulrush (*Scirpus acutus*) are the dominant aquatic plant species. Sizeable stands of whitetop (*Scolochloa festucea*) and three-square bulrush (*Scirpus americanus*) are also present. Horned pondweed (*Zannichellia palustris*) and water milfoil (*Myriophyllum* sp.) occur but are not abundant. Many halophytes are common along shorelines.

Stomach Contents—Seeds and fruits of aquatics formed the main diet of 122 adult pintails examined by us (Table 1). Identifiable remains of insects and other invertebrates constituted less than 5 percent of the total volume of organic matter ingested. Alkali bulrush, sago pondweed and hardstem bulrush comprised over 98 percent of the identifiable plant material. The latter two species are recognized as key duck foods in many sections of North America. The local importance of alkali bulrush as a waterfowl food has been noted previously (Wetmore, 1921; Addy, 1946; Yocum, 1951). However, in view of its heavy utilization at Pel Lake, and its abundance in countless other saline waters across the prairies, we wonder if perhaps the value of alkali bulrush, particularly during summer, has not been greatly underrated.

The volume of grit in each gizzard was found to average 1.31±0.07 ml. Fifty-six percent of the gizzards contained between 0.95 ml. and 1.54 ml. of grit (Fig. 1). Grit was separated into three size groups using 1 mm. and 2 mm. sieves. Average quantities of grit per group were as follows: >2

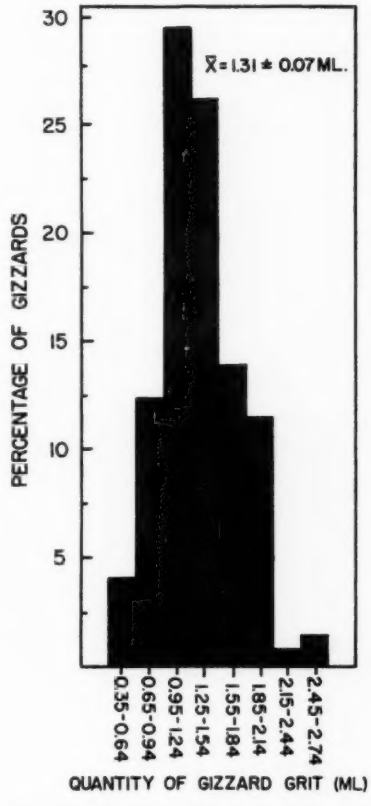

FIG. 1. Distribution of gizzard-grit volumes from 122 adult pintails.

[1] The cooperation and financial assistance of Ducks Unlimited (Canada) and the Delta Waterfowl Research Station, Delta, Manitoba, is gratefully acknowledged. R. A. McCabe kindly read and commented on the manuscript.

TABLE 1.—STOMACH CONTENTS OF FLIGHTLESS ADULT PINTAILS FROM PEL LAKE, SASKATCHEWAN[1]

Scientific Name	Common Name	Percent Volume	Percent Occurrence
IDENTIFIABLE PLANT MATERIAL[2]			
Scirpus paludosus	Alkali bulrush	32.4±6.9[3]	94
Potamogeton pectinatus	Sago pondweed	14.5±4.8	65
Scirpus acutus	Hardstem bulrush	9.5±2.8	47
Eleocharis palustris	Spike-rush	0.1	22
Chenopodium sp.	Goosefoot	0.1	21
Polygonum sp.	Smartweed	0.1	10
Ceratophyllum demersum	Coontail	0.1	2
Zannichellia palustris	Horned pondweed	tr.	9
Rumex sp.	Dock	tr.	6
Carex sp.	Sedge	tr.	5
Myriophyllum sp.	Water milfoil	tr.	2
Triglochin maritima	Arrowgrass	tr.	1
Gramineae	Grass	tr.	1
Total		57.1	
ANIMAL MATTER[4] AND UNIDENTIFIED ORGANIC MATERIAL			
Insecta	Insects		46
Cladocera *Daphnia* sp.	Waterflea (egg cases)		35
Gastropoda	Snails		1
Unidentified finely ground organic material			100
Total		42.9	

[1] Stomachs from 115 males and 7 females collected July 9, 1957.
[2] Seeds or fruits.
[3] 95 percent confidence limits.
[4] Estimated at less than 5 percent by volume.

mm. — 0.21±0.03 ml.; 2 mm. to >1 mm. — 1.05 ±0.08 ml.; ≤1 mm. — 0.05±0.04 ml.

Weights—Weights of flightless adult pintails shown in Table 2 probably equal or approach the yearly minimum for this species (Baldwin and Kendeigh, 1938; Bennett, 1938; Weller, 1957). The average live weight of 69 males was 31.4±0.5 oz.; 116 other males averaged 30.1±0.5 oz., 40 to 55 hr. after death. Bellrose and Hawkins (1947) reported the mean fall weight of 237 adult pintail drakes shot along the Illinois River as 2.28 lb. (36.5 oz.). Mann, *et al.* (1947) gave 2.09 lb. (33.5 oz.) as the average of 188 adult pintail drakes trapped at McGinnis Slough, Illinois. Seven adult females weighed 25.7±1.4 oz. (Table 2) compared to 1.96 lb. (31.4 oz.) for 60 adult females handled by Bellrose and Hawkins (1947).

TABLE 2.—WEIGHTS OF FLIGHTLESS ADULT PINTAILS TAKEN AT PEL LAKE, SASKATCHEWAN, JULY 9, 1957

Age Class	Live Wt. (oz.)	Dead Wt.[1] (oz.)	
	Males	Males	Females
≧ 1 yr.	31.2±0.9(24)[2]	30.1±0.5(116)	25.7±1.4[3](7)
≧ 2 yr.	31.2±1.4(17)		
≧ 3 yr.	31.7±1.1(19)		
≧ 4 yr.	31.9±1.3 (9)		
Avg. wt.	31.4±0.5(69)		

[1] 40 to 55 hr. post mortem.
[2] Sample size.
[3] 95 percent confidence limits.

Though lacking statistical significance, there is some indication (Table 2) that weights of adult males increase slightly with age.

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THE CANADA GEESE OF MICHIGAN'S SWAN CREEK HIGHBANKS, 1953–1957[1]

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The Swan Creek "Highbanks," a public goose-shooting area in southwestern Mighigan, for several years has been providing information on the Canada geese (*Branta canadensis*) migrating down the east shore of Lake Michigan. The data presented here complement those in my paper on controlled goose shooting and harvest at the Highbanks (Friley, 1959) at the North American Wildlife Conference. They were obtained from examination of 6,618 geese shot at the Highbanks during the hunting seasons of 1953 through 1957. We recorded age and sex of 6,550 of these geese (the remainder were mutilated by shot), and separated immature birds (birds of the year) by their worn, notched tail feathers. We did not distinguish between adults and subadults. In this paper I group them together and refer to them as "adults." We have good data on the sexes in all years but 1956, when we had to discard sex data for 1,010 birds examined because of errors in sexing by one examiner.

the Highbanks since 1953 lie in a narrow band from Akimiski Is. in James Bay in northern Ontario to Crab Orchard and Horseshoe Lakes in extreme southern Illinois, between the Jack Miner Sanctuary in southern Ontario at the west end of Lake Erie and Horicon Marsh in eastern Wisconsin. The flock winters from the Swan Creek area southward to the federal and state refuges in southern Illinois.

Goose Weights

Highbanks geese were slightly heavier than November and December birds from Horseshoe Lake, Illinois, examined by Elder (1946). The average weight of our 6,550 geese was 7.97 pounds. "Adult" birds (8.48 lb.) weighed about a pound more than immatures (7.37 lb.), and males ("adults" 9.04 lb.; immatures 7.90 lb.) about a pound more than females ("adults" 7.82 lb.; immatures 6.86 lb.). Adult females and immature males were nearly the same weight. The average adult male weighed about a pound greater than the mean for all geese, and the average immature female, about a pound less. Average weights of geese in 1953 (7.76 lb.) were about one-quarter pound less than in the following 4 years (7.96–8.04 lb.). This was true for all sex and age classes. Possibly the birds were in poorer condition in 1953 when they arrived from the north than in succeeding years. From 1954

Table 1.—Canada Geese in the Lower Kalamazoo River Area, 1953–1957

Season	Fall Arrival		Peak Population		Wintering Population	Spring Peak Numbers	Final Departure Date
	First Arrival	1,000 Present By	Number	Date			
1953–54	Aug. 23	Oct. 30	3,000	Nov. 2–5	1,000	–	–
1954–55	Sept. 20	Oct. 10	11,500	Nov. 9	6,000	8,000	April 17
1955–56	Sept. 21	Oct. 24	15,000	Nov. 22	8,000	16,000	April 21
1956–57	Sept. 29	Oct. 5	9,000	Dec. 3	6,500	20,000	April 27
1957–58	Sept. 25	Oct. 21	11,500	Nov. 25	6,500	13,000	April 23

The Highbanks, described by Friley (1959), is a part of the Swan Creek Wildlife Experiment Station of the Michigan Department of Conservation, 9 miles northwest of Allegan in the Allegan State Forest. The station is first of all a place for research on wildlife problems, and secondarily a 7,000 acre area open to managed public hunting. Table 1 presents a brief picture of the migration dates and numbers of geese involved.

Bands recovered from geese shot at the Highbanks indicate that Swan Creek geese are from an eastern component of the Mississippi Valley flock, described by Hanson and Smith (1950). Banding stations for all but 1 of 152 banded geese bagged at

Table 2.—Weight Increase of Canada Geese Shot at the Swan Creek Highbanks from Early October to Late November, 1953–1957

	Weights in Pounds				
	Age		Sex		All Geese
	Adult	Immature	Male	Female	
1953	0.62	0.70	0.97	0.72	0.82
1954	0.65	0.46	0.80	0.47	0.68
1955	0.93	0.95	1.11	0.93	1.11
1956	0.82	0.63	–	–	0.62
1957	0.18	0.19	0.39	0.07	0.20

[1] A contribution from Federal Aid in Wildlife Restoration Project W-89-R, Game Division, Michigan Department of Conservation. C. H. Douville and H. L. Wilson were leaders of the project. The staff of the Swan Creek Wildlife Experiment Station collected the data. The writer thanks C. T. Black and H. J. Miller for assistance in preparation of the manuscript.

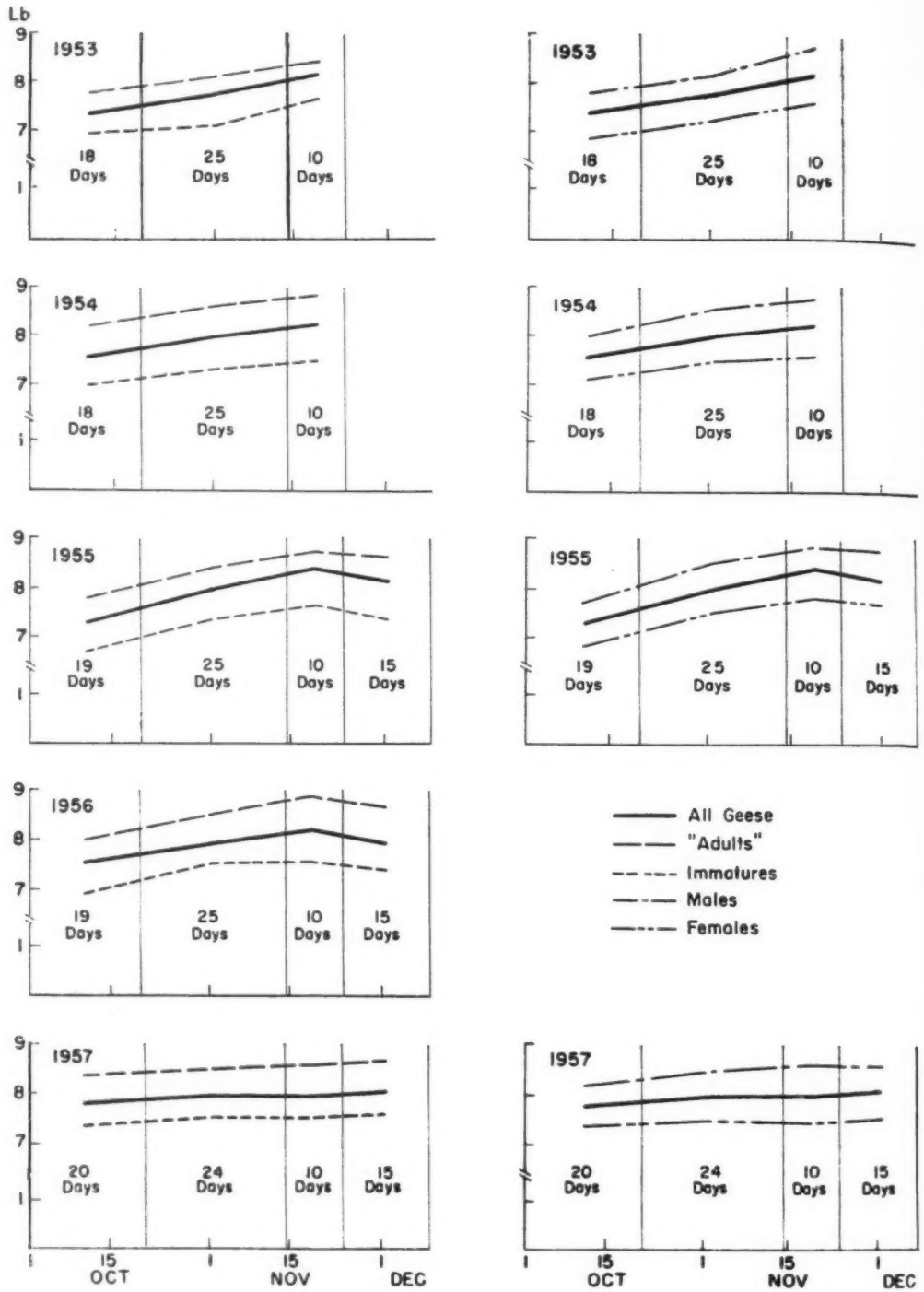

FIG. 1. Seasonal variation in weights of Canada geese shot at Swan Creek Highbanks, 1953–57.

TABLE 3.—SEX AND AGE DISTRIBUTION AND RATIOS IN THE HIGHBANKS CANADA GOOSE HARVEST (1953–1957)

	SEX			AGE		
	Male	Female	Males per 100 Females	Immature	Adult	Immatures per 100 Adults
1953	361	334	108.4	257	438	58.4
1954	814	842	96.7	789	867	91.0
1955	817	787	103.8	598	1,006	59.4
1956	–	–	–	550	460	119.6
1957	782	803	97.4	864	721	119.8
Total	2,774	2,766	100.3	3,058	3,492	87.6

through 1957 geese were slightly heavier, and average weights varied scarcely at all. This relationship prevailed in all sex and age groups (Fig. 1).

In 4 of the 5 years, geese shot early in the season were lighter, and those shot later on were heavier (Fig. 1). On the average, weights of Swan Creek geese increased between two-thirds of a pound and just over a pound, from early October to late November, each year from 1953 through 1956 (Table 2). In contrast, weights in 1957 during this period remained nearly the same (less than a quarter of a pound increase). Again, neither age nor sex appeared to influence weight increases of geese during the fall. All age and sex groups increased at approximately the same rate in any given year. In 1955 and 1956, when the hunting season extended into early December, weights declined at the end of the season. In 1957, December weights failed to decline. Fall weight gain may be simply a reflection of the abundance of food available in the Swan Creek Marsh and at the Fennville State Game Area, but to interpret these weight changes more intelligently we need to know more about how many individuals pass through our area and how long the different flights stay with us.

SEX AND AGE OF GEESE

The sex ratio in 5,540 Canada geese (year 1956 excluded) was nearly even, about what one would expect in a population where hunters make no attempt to select males over females. The average ratio in the 4 years with accurate data was 100.3 males per 100 females, with minor variation from year to year (Table 3).

Wide variation in the age ratios occurred through the 5 years around a mean of 87.6 immature birds per 100 adults (Table 3). Extremes were 58.4 immatures in 1953 and 119.8 in 1957. Because of the lumping of adults and subadults in the "adult" class, because Swan Creek geese form only a portion of the Mississippi Valley flock, and because the turnover in the Highbanks flock during the fall is unknown, one cannot interpret these figures as echoing differences in productivity in the flock as a whole.

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THE USE OF CARIBOU ANTLER PEDICELS FOR AGE DETERMINATION

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While storing caribou skulls for a taxonomic study, I discovered a method of age determination that would seem to merit consideration. Because of the difficulties in storing these skulls, it had been decided to remove the antlers. In doing so, I noticed the form and variety of pedicels. The annulations that appeared in cross-sections were particularly interesting. I decided to study them in a series of caribou (*Rangifer*) skulls of various ages in order to determine their significance.

METHODS

The variations in pedicel length and girth between the frontal bone and the burr were noted and correlated with sex, age, and antler form. Pedicel transverse sections about one-quarter inch thick were cut with a diamond rotary saw. One surface was polished with a series of rotary emery stones and finally on a nylon buffing wheel as in standard lapidary practice. The sections were then

examined under a low-power (15×) binocular microscope.

OBSERVATIONS

Both sex and age were observed to influence pedicel form. Males carried pedicels and burrs of greater girth than females. The pedicels of younger animals appeared longer and slimmer than those of older ones. The apparent shortening of the pedicels with increasing age was largely an illusion because it was accompanied by an increase in girth and a thickening of the frontal bones, although there may be some resorption of bone at the burr when the antlers are shed (Wislocki and Waldo, 1953). The deposit of bone on the pedicel with increasing age offered a possible mechanism for age determination.

Study of the pedicel sections indicated a series of alternating dark and light rings. On the other hand, antler sections showed, about the core, only one dark ring which gradually faded toward the periphery.

A series of pedicel sections was prepared from caribou skulls of known ages in order to test the hypothesis that the rings were annual deposits. The series was composed mainly of younger animals aged from 6 months to 3 years whose age could be determined accurately by tooth eruption and wear (Banfield, 1954). The results of the comparison between ages determined by teeth and by pedicel annulations are given in Table 1. The agreement in the two methods permits the following description of growth.

In the genus *Rangifer*, both sexes generally carry antlers that begin to grow during the first summer of the fawn's life. Knobs develop early on the frontal bones. As the season progresses there is a deposit of soft dark vacuolated bone under the richly vascularized velvet which forms a slender shaft 6 to 12 inches long (the spike horn). That core is similar to the dark vacuolated bone found in the mandibles and leg bones of young reindeer in summer, referred to as "black bone" by herders and attributed to the soft summer diet.

In autumn the burr forms as a ring well up on the shaft beyond which the velvet is rubbed off and the antler emerges. Below the burr, however, the pedicel continues to receive nourishment beneath the vascularized skin. A narrow ring of paler finer-grained bone is deposited about the core during the winter. Eventually the antler breaks off at the burr in late spring.

A second pair of antlers is grown during the second summer. Again a darkly pigmented ring of bone is deposited under the vascularized velvet around the pedicel, and the new antler takes shape on top of the burr. The velvet of the second antler loosens and is dropped during the second autumn, and a second layer of paler bone is deposited about the darker band after antler growth is terminated. The girth of the pedicels continues to grow with increasing age through the deposit of alternating dark and light rings, although the annual increments lessen as indicated in Figure 1.

Unfortunately, two other processes that tend to obscure the regular annual rings occur. In the first place, the pigmented rings laid down during antler

TABLE 1.—COMPARISON OF ESTIMATED AGES OBTAINED FROM TOOTH ERUPTION AND PEDICEL ANNULATIONS

Month Taken	Tooth Eruption	Tooth Wear on M_3 post. cone	Estimated Age by Teeth	Number of Dark Rings	Outside Light Ring Present	Estimated Age by Rings
Dec.	M_1	–	6 mo.	1	×	1 year
Apr.	M_2	–	10 mo.	1	×	1 year
Apr.	M_2	–	10 mo.	1	×	1 year
Apr.	M_2	–	10 mo.	1	×	1 year
July	$PM_{2,3,4}$	–	13 mo.	1	×	1 year
Aug.	M_2	–	14 mo.	2	–	1 yr.+
Sept.	M_3	–	15 mo.	2	–	1 yr.+
Sept.	M_3	–	15 mo.	2	–	1 yr.+
Mar.	M_3	–	21 mo.	2	×	2 yrs.
Apr.	M_3	–	22 mo.	2	×	2 yrs.
?	Complete	none	2–3 yrs.	2	×	2 yrs.
Aug.	Complete	none	26 mo.	3	–	2 yrs.+
Sept.	Complete	none	27 mo.	3	–	2 yrs.+
Oct.	Complete	light	2–3 yrs.	2	×	2 yrs.+
Apr.	Complete	light	2–3 yrs.	2	×	2 yrs.
Apr.	Complete	light	2–3 yrs.	2	×	2 yrs.
Sept.	Complete	light	2–3 yrs.	3	–	2 yrs.+
Oct.	Complete	light	28 mo.	3	×	3 yrs.+
Oct.	Complete	moderate	2–3 yrs.+	3	×	3 yrs.+
Dec.	Complete	light	2–3 yrs.	3	×	3 yrs.+
Dec.	Complete	moderate	2–3 yrs.+	3	×	3½ yrs.
Oct.	Complete	moderate	adult	4	–	4 yrs.+
Oct.	Complete	moderate	adult	4	×	4 yrs.+
Nov.	Complete	moderate	adult	4	×	4½ yrs.

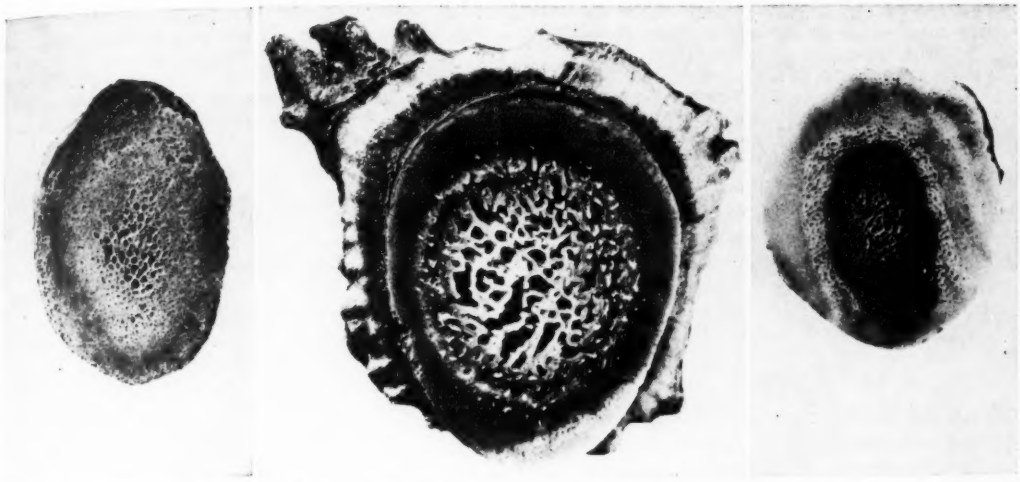

FIG. 1. Transverse sections of caribou pedicels from a 1-year-old bull (left), a 2½-year-old bull (middle), and a 3½-year-old cow (right). Magnification 2×.

growth tend to fade with increasing age. Secondly, additional bony material is deposited in the structure so that the vacuolated cells become more consolidated. No more than four dark rings have been noted in specimens used in this study.

DISCUSSION

When my interest in the subject was first aroused, I looked for a good description of the physiology of cervine antler development. Wislocki (1943), Waldo and Wislocki (1957) and Wislocki and Waldo (1953) investigated the annual cycle on antler growth and shedding. Although they examined the histology of the pedicel-antler junction they paid little attention to the structure of the permanent pedicels.

The use of fish scales and mammal tooth cement for age determination depends upon the occurrence of a factor with regular annual discontinuities such as feeding habits. Antler formation in cervids also provides an annual discontinuity suitable for age determination.

Although the preliminary study was conducted with caribou, pedicel annulations were also observed in other species of deer (*Odocoileus, Cervus,* and *Alces*) in which the technique may be useful also for age determinations.

The present sectioning technique is not entirely satisfactory. It is likely that thinner sections, stains, and higher magnification may reveal more significant cellular structure. At present the method seems to have limited use up to about the fifth year. It complements, however, other methods such as tooth eruption and wear (Severinghaus, 1949; Quimby and Gaab, 1957) and tooth sectioning (Fisher and Mackenzie, 1954).

There are two other fields of research to which this technique may be applied. The width of the annual rings may be used to assess the nutritional level of a particular year. Wide rings, by the deposit of a large amount of bone, would indicate a high nutritional plane, and narrow rings would indicate seasons of restricted food.

Hawthorn and Duckworth (1958) have recently shown that fall-out radioactivity may be detected in deer antlers. Using the pedicels of large males, sections of excised bone might be analysed independently to provide data on fall-out radioactivity over a number of consecutive years.

The exaggerated length of the pedicels of some young cervids, especially yearling wapiti *Cervus,* is reminiscent of the tall pedicels of certain extinct Tertiary genera such as *Dromomeryx* and *Cranioceras.* One wonders if youthful age of the extinct specimens might not be a factor which could be clarified by examination of the teeth.

CONCLUSION

A preliminary study of caribou pedicel sections has indicated the presence of annual rings during and after antler formation which provide a method of age determination that merits further study in other cervids.

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NOTES ON USE OF CLOVER ONE-SHOT DEER MARKER

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During a study of Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) on western Montana summer range, various methods were used in attempts to mark deer individually. The Clover one-shot marking guns (M.R. Clover, 1954. Deer marking devices. Calif. Fish and Game, 40(2): 175–181.) were found most successful. However, three difficulties in the use of these guns were encountered and overcome: sealing compound; marking liquid; positioning of the guns.

Ordinary vaseline proved to be the most effective sealing compound tried. It was easily melted and poured into the open end of the water-pipe chamber on top of the propelling shotgun shell at the other end; a cork dipped in vaseline was used to seal the open end. The vaseline maintained an effective seal even with warm daytime and freezing nighttime temperatures; the possibility of sunlight melting the vaseline and destroying the seal was avoided by shading the markers with vegetation.

Saturated water solutions of basic fuchsin and malachite green were used for marking in 1957. Ethyl alcohol was added to prevent freezing and liquid detergent was added to dissolve the hair oils. In outdoor tests with fresh mule deer hides, the basic fuchsin and malachite green applications appeared visible for only two to three weeks; this may have been why no marked deer were seen in 1957, although 15 possible animals were marked, as evidenced by successfully fired markers. Marking solutions of diamond black, methylene blue chloride and gentian violet blended with the normal winter-coat hair color of the hides. In 1958 aluminum paint was used as the marking fluid. Its varnish vehicle appeared to mat the hair less than regular paints with their lead and oil vehicle. This paint was easily visible 8 weeks after application on a winter-coat hide kept outside on the roof of a building. Fifteen possible animals were again marked in 1958. One marked adult doe mule deer was observed on the summer range, the aluminum paint clearly and quickly visible at ½ mile through 7 × 50 binoculars. A sketch of the paint pattern, made from observation with 60× spotting scope, appeared sufficiently unique to differentiate it from other potential markings.

The tests with fresh hides indicated at least 25 cc. of marking fluid was necessary to produce good markings. This required use of an 8-inch length of water pipe for the marking gun.

To facilitate identification of marked deer the markers were set up on game trails in pairs, to mark the deer on both sides simultaneously. A single trip cord was used for one pair of markers. Moving the markers after one or two successful firings resulted in greater potential marking success; on two occasions observations after snowfall revealed that both deer and elk walked to within 2 feet of trip-cords of previously fired guns and then abruptly left the trails, to return only a few yards beyond the markers. Potential marking success was also increased by nailing the markers to trees rather than utilizing stakes driven into the ground; the firmer support prevented kicking-up of the markers upon firing. The effective muzzle height for deer appeared to be 30 inches above ground. Experimental firing of markers revealed that compact yet distinctive paint patterns on deer hides were secured when the muzzle was no more than 2½ feet from the target.

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DETERMINING ELK MOVEMENTS THROUGH PERIODIC AERIAL COUNTS[1]

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This paper presents a report on the use of periodic aerial surveys to ascertain elk movements and migration patterns. As an attempt to add to the store of knowledge relating to the elk of Idaho, the Idaho Fish and Game Department and the Idaho Cooperative Wildlife Research Unit initiated a study in the Selway-Bitterroot Wilderness Area of north central Idaho (Robel, 1958).

Aerial censusing of big game populations is a common practice of most game departments. Ruhl (1932) felt that aerial censusing was too expensive to be practical in wildlife management. Later, as flight time became less expensive and the value of wildlife became more apparent, aerial censusing of most big game animals evolved into an acceptable technique. The applicability of aerial censusing is dependent upon many factors, including terrain, cover, etc. Matteson (1950) reported that by 1950, most states with elk populations were using airplanes to census their herds.

In many instances, the knowledge of an elk population size alone is not sufficient for an intelligent management program. An insight into migration routes and the time of these migrations is at times extremely valuable to the big game manager. In an attempt to develop methods to obtain this information, both air and ground surveys of elk were conducted in the Selway district of Idaho in the winter of 1957–1958.

Methods

Every 2 weeks, systematic aerial surveys of the study area were carried on during the mid-November, 1957 to mid-June, 1958 period. Two types of airplanes were used: a Cessna 180 and a Super Piper 125.

Aerial surveys were made lengthwise of the 150-square-mile study area, following the course of the Selway River. The flight pattern consisted of flying upstream along the mountainsides at one elevation and then returning along the study area at a lower elevation. The higher flight made possible the observation of animals in the 3,000- to 4,000-foot elevational belt. The second flight was made at about 2,500 feet and covered the area between 2,000 and 3,000 feet. The plane entered every small drainage, following closely the contour of the steep mountains. These two transects enabled both logitudinal and elevational calculations of elk distribution.

Maps with a scale of ½ inch per mile were used by the observer in the plane to record locations of herd concentrations and numbers of elk sighted.

In conjunction with the aerial surveys, ground surveys were conducted on the same study area. Every 2 weeks, hikes were made along the 30-mile length of the study area. Frequent side trips were taken up minor ridges to obtain observations of elk at higher elevations.

Results

The data obtained from each aerial and ground survey were stratified into eight categories, consisting of 4-mile sections of the survey route. Since differences in census conditions (snow cover, light intensity, weather, time of day, etc.) caused variations in the total number of elk observed during each trip, elk numbers for each category were converted to percentages of the total animals observed in that trip. Percentage distribution graphs were then constructed to show changes in the locations of the elk herd concentrations.

The actual number of elk observed during each trip varied greatly. In total, 1,777 elk were sighted during 8 aerial surveys, while 481 elk were observed during 5 ground surveys. The number of elk sighted during each trip was closely correlated with ground cover, weather conditions, and light intensity. Highest counts were made (close to 90 percent of the elk present on the study area) when the ground was covered with a solid blanket of snow, temperatures were above freezing, and a high cloud cover lowered the light intensity.

Although the number of elk observed during the aerial surveys exceeded those sighted by the ground survey team, the movement results were very similar. Final plotting of elk concentration areas and dates of movements were almost identical.

Discussion

By plotting migration routes, the summer range of a large elk herd which was causing severe damage to a portion of the winter range was discovered. Since the time of migration was also determined, it might well be possible to set the hunting season to intercept the migrating herd as it moves from its summer range to the wintering area. However, further studies must be undertaken to determine whether or not these routes and dates remain constant from one year to the next. The study found the periodic aerial surveys to be an efficient way to detect and measure such movements.

Summary

In an attempt to determine elk migration routes and the time of these migrations in the Selway dis-

[1] Contribution from Pittman-Robertson Research project W 85-R-9 Job No. 3, the Idaho Department of Fish and Game and the Idaho Cooperative Wildlife Research Unit cooperating.

trict of Idaho, aerial and ground surveys were conducted every other week during the mid-November, 1957 to mid-June, 1958 period. Observations of elk were then plotted and mapped on a percentage basis. Both aerial and ground survey data proved to be quite similar. Thus the aerial surveys were found to be useful in tracking migrating herds of elk.

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A COLOR MARKING TECHNIQUE[1]

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Two problems encountered in the color marking of birds are the difficulty of capturing enough birds for marking and the fact that many birds "desert" when trapped at their nest. Heretofore, such trapping has been unavoidable for certain studies. The technique reported here seems to offer a solution to these problems. This technique consists of placing a powdered, water soluble dye on the eggs and nest. The parent birds become dyed when the powder in contact with their feathers is moistened.

A. Dean Paddock, Bob Harris and N. E. Fine assisted by watching for and recording marked birds.

On July 20, 1959, the eggs and, unavoidably, also the nests of about 30 pairs of glaucous-winged gulls found on an island in Lake Nerka, about 40 miles north-northwest of Dillingham, Alaska, were treated with "Thief Detection Powder."[2] An estimated two or three cubic centimeters of the powdered dye were applied to each clutch. Ten days later, on July 30, it was possible to count 16 purple-colored birds in the flock milling over the nesting area. The posterior parts of their bellies and, on some birds, the anterior under tail coverts, showed the dye. There could well have been more dyed birds because some of the gulls were sitting on the water and others could have escaped observation in the wheeling flock or have been temporarily absent from the colony.

On August 3 the island was checked again and from the flock, many of which were colored, a single adult female was collected (Fig. 1). This bird was neither the most, nor the least, heavily dyed. Of the obviously dyed birds, it seemed about average. In addition to the ventral coloration, which did not involve the under tail coverts, it had small spots of purple on its wings, especially on the leading edge from the bend of the wing distally.

FIG. 1. Adult female glaucous-winged gull. Dark coloration on its belly is actually a bright purple stain produced by powdered dye sprinkled on its eggs.

Although the eggs were brilliantly purple, there was no obvious egg loss either from desertion or predation. Coloring of the eggs, however, might militate against use of the technique in some cases. None of the hatchlings showed purple coloration.

It remains to be seen how long the dye will last, and whether or not this technique will work on other species. Also, experiments should be made with other dyes. While these results are of a very preliminary nature, the technique is reported now because it appears to have considerable promise as a research tool.

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[1] A research contribution of the Alaska Department of Fish and Game, Juneau, Alaska.

[2] Obtained from Faurot, Inc., 299 Broadway, New York, N.Y.

A NOTE ON JUVENILE MOURNING DOVE POPULATIONS AT WEST PALM BEACH, FLORIDA[1]

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During the period March 1950 through February 1958, C. C. Anderson banded and aged 14,406 mourning doves (*Zenaidura macroura*) at West Palm Beach, Florida. An interesting characteristic of these data is the high monthly percentages of juveniles in the unbanded adult–juvenile samples during the major portion of each year.

This paper is concerned with the trend in the percent of newly banded birds that were juveniles during the period March through February, as well as a comparison of individual period trends through the 8 years of banding. The primary purpose of this paper is to determine whether or not the eight yearly trends of percent juveniles in the unbanded adult–juvenile sample (March through February) can adequately be described by one curvilinear regression line, rather than to speculate on the population characteristics which are reflected in these data.

Sample Characteristics

The trapping station at West Palm Beach was an old baseball field with a catcher's backstop utilized as a perch by doves. An ample supply of bait was available to the birds at all times. Trapping was conducted in the afternoon every 3 or 4 days. During the 8-year period, doves were banded in all months except August and October 1950 and March 1952. The mean numbers banded and their standard errors for months, years, and the overall sample of 93 months are 1200.5 ± 175.0; $1{,}800.8 \pm 208.1$; 154.9 ± 12.6, respectively. As was to be expected, the smaller samples were obtained during late winter and early spring each year. With the exception of the 1950–51 period when 867 birds were banded and aged, over 1500 birds were banded each year. The number of birds trapped during the 93 trapping months ranged from 17 to 747, with more than 100 birds being banded each month during 53 of these months. The raw data are on file at the Patuxent Research Refuge, Laurel, Maryland.

A graphical inspection of the data revealed that in all years the percent of newly banded birds that were juveniles was in general low during March, and by May exceeded 90 percent. Percentages in excess of 90 percent were characteristic of the period May through November, after which percentages in four of the periods decreased rapidly to March. During the other periods, 1953, 1955, 1956 and 1957, the January and February samples of non-banded birds contained 90 percent or more juveniles.

The question of interest to be discussed in this paper is whether or not the trend in percentage of juveniles in the unbanded population from March through February is essentially the same each year in the West Palm Beach area; i.e., can deviations from an average trend be attributed to sampling error?

Methods and Results

A statistical analysis of the data was conducted to determine if the trend in percent of newly-banded birds which were juveniles over the eight 12-month periods (March through February 1950–1958) could be adequately described by one polynomial regression line. Upon inspection of the data it was obvious that the trend through each period could adequately be described by a second-degree polynomial equation. Hence, the regression model was

$$y = \beta_0 + \beta_1 x + \beta_2 x^2 + \epsilon \ ,$$

where y is the dependent variate, percentage of juveniles (transformed to arc-sine); x is the fixed independent variant, month; β_i, the i^{th} regression coefficient (i=0, 1, 2); and ϵ, the residual error. The errors are assumed to be normally and independently distributed around the population regression line with homogeneous variances. All percentages were transformed to arc-sines. Rather than use a more complicated procedure, the three missing values were computed merely by taking the average for the month in which the missing value occurred and the appropriate degrees of freedom were reduced by 3. The regression equations were fitted by means of orthogonal polynomials utilizing unweighted percentages. An appropriate procedure to determine whether or not the overall data can adequately be described by one regression line rather than one for each period involves (1) computing the total sums of squares of deviations around the eight fitted individual regression lines, (2) computing the sum of squares of deviations around the overall regression line, and (3) determining whether or not there has been a statistically significant reduction in the sum of squares of deviations as a result of fitting the eight individual regression lines.

Results of this analysis of variance are presented

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TABLE 1.—RESULTS OF AN ANALYSIS OF VARIANCE TESTING WHETHER OR NOT THE DATA CAN BE SUITABLY DESCRIBED BY ONE QUADRATIC REGRESSION LINE

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Deviations from individual period quadratic regressions	69	6,426.77	93.14	
Reduction due to fitting individual period regressions	21	8,517.96	405.62	4.35[1]
Deviations from overall quadratic regression	90	14,944.73		

[1] Significant at the 1 percent level of significance.

in Table 1. It is seen that there is a significant reduction in the sum of squares as a result of fitting individual quadratic regressions. Therefore, it is concluded that the yearly trends in the percent of juveniles in the unbanded adult–juvenile monthly populations were not the same during the eight periods studied. An inspection of a graphical plot of these data discloses that the major differences occur in late winter and early spring. For example, the percentages for March ranged from 4.5 percent in 1950 to 94.1 percent in 1958. These percentages probably reflect nesting success and sampling intensity. During the period June through November the monthly sample percentages were never less than 85 percent, with 40 out of 46 months, where samples were collected, consisting of over 90 percent juveniles.

The reader should not draw the conclusion from these data that the percentage of juveniles in the mourning dove population at West Palm Beach was extremely high during the study period. It must be kept in mind that the percentages discussed involve only *unbanded* birds; thus, adults captured early from a non-migratory population and recaptured would only affect the percentage at the initial capture. Similarly, juveniles banded early in the nesting season would not influence percentages when recaptured, regardless of whether or not they were still juveniles or had become adults. The high percentages of juveniles of the newly-banded birds in late fall are not necessarily an indication of late nesting success but may be merely a reflection of juveniles in the migrant population. The lack of banding records for this group prevents elaboration of this point.

SKIN LESIONS ON BLACK DUCKS AND MALLARDS CAUSED BY CHIGGER (*WOMERSIA STRANDTMANI* WHARTON 1947)

Gordon M. Clark and Vernon D. Stotts

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Extensive skin lesions were noted around the vents of a number of black ducks (*Anas rubripes*) and mallards (*Anas platyrhynchos*) trapped in the Kent Island area of Chesapeake Bay in late August and September of 1957 and 1958. All the affected birds were young of the year that quite probably had hatched in the immediate vicinity of Kent Island. This condition was obvious in 10 percent of 443 juvenile black ducks and 8 percent of 60 juvenile mallards checked September 20–October 24, 1957.

Eight birds with severe skin inflammation were examined at the Henshaw Disease Laboratory. All showed numerous raised vesicles, ranging from 1.5–3.0 mm. in diameter, on the skin of the venter. These lesions extended forward from the tail, around the cloaca, and up the large ventral feather tracts to an area high on the breast. The feathered skin of the legs was also severely inflamed.

Feathers in the heavily infested areas were somewhat sparse. Birds with less heavy infestations appeared normal and it was necessary to clip away feathers in order to observe the area of damage.

Stereoscopic examination (45×) of the blister-like vesicles showed that each contained one, or occasionally as many as five, tiny pits. A chigger, or larval stage of a trombiculid mite, was seen to be deeply imbedded in each pit, with only the extreme posterior tip of the abdomen visible. The skin of the vesicles and the surrounding area was red and inflamed. Often the vesicle itself was reddish purple in color as a result of tissue digestion by the chigger.

In order to illustrate more fully the tissue damage, microscopic sections were cut from formalin fixed vesicles biopsied from live birds. Each chigger was seen to be completely imbedded in the skin (Figure 1). Such deep penetration seems to be characteristic of the apoloniid group of chiggers, as it was reported by Carneiro (1949). The mite is surrounded by a tough leathery sack, the histiosiphon. This envelope of keratinized or chitinized material

FIG. 1. Section of black duck skin showing an embedded, feeding chigger.

becomes quite tough on fixing. For this reason it is often shattered in the preparation of sections. At the bottom of the histiosiphon is a tiny tube, the stylosome. This is the feeding tube of the chigger, down which digestive enzymes are pumped. These liquefy the host tissue, and the fluid material then is pumped back up the tube and into the gut of the mite. It is quite likely that both histiosiphon and stylosome are secretory products of the mite rather than host reaction phenomena.

The host tissue immediately below the stylosome shows intense liquefaction necrosis. There is pycnosis and karyorrhexis of cell nuclei and the area is left almost free of cell structure. Farther from the immediate area of digestion there is extensive infiltration by heterophyll leucocytes and considerable fluid is present. Still farther from the chigger the vesicle is composed chiefly of collagenous tissue.

Careful study and measurement of 25 chiggers recovered from the pits indicated that, although larger, they were morphologically indistinguishable from *Womersia strandtmani* Wharton 1947, which has been found previously only on a brown pelican (*Pelecanus occidentalis*) in Galveston, Texas (Wharton, 1947).

Large numbers of live, unharmed chiggers may be collected if an infested bird is killed and placed immediately in a wire cage over a flat pan of water. Chiggers leaving the bird fall through the wire and come to rest on top of the water. As many as 200 of the small, bright orange mites have been recovered from a single bird by this technique. If the larvae are fully fed, they may be stored in small vials at a high relative humidity, where transformation to the nymphal stage will occur.

If infested ducks are held alive in wire cages over water-filled collecting trays in the laboratory, the chiggers leave the birds quite slowly. Two birds were held thus from September 20, 1958 to February 15, 1959, at which time both birds still harbored many chiggers. It has not been determined when the chiggers normally leave the bird under field conditions. The fact that chigger damage has not been noted in the field during winter months is some indication that chiggers do not take so long to feed under natural conditions.

Infestations of this mite generally can be diagnosed in the field by feeling the legs of the duck at the junction of scaly and feathered skin. If the duck harbors many mites, vesicles can be felt as distinct bumps in this area.

Since heavy attack by this chigger clearly is highly irritating and perhaps toxic to ducks, further studies on this parasite are planned. We are particularly interested in determining the range of this mite, the area of initial infestation, whether other duck species are infested, and how long chiggers remain on ducks in the field.

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OBITUARY

RICHARD BIRNIE MILLER
1915–1959

The untimely death of Richard Birnie Miller on February 23, 1959, deprived Canada of one of her most stimulating fishery biologists in the full spate of a vigorous scientific career. Dr. Miller was born on March 29, 1915, in Weyburn, Saskatchewan. He was the son of Judge Moore Armstrong Miller and Caroline Muriel Birnie. He married Lillian Frances Harkness in 1937 and is survived by his wife and two children, Richard G., and Frances A. E.

Dr. Miller received his public and secondary school education in Saskatchewan and then entered the Honour Biology Course at the University of Toronto. On graduation in 1936 he was awarded the G. A. Cox gold medal in Biology. His graduate training was also taken at the University of Toronto. He was awarded his master's degree in 1937 and his doctorate in 1939. He was a brilliant and hard-working student. His graduate work was concerned with the ecology of the Chironomidae. He went to the University of Alberta as a lecturer in zoology in 1939 after the completion of his graduate work, and advanced through assistant and associate ranks to professor in 1952, and Head of the Department in 1956. His students remember him as a vigorous and inspiring teacher, both at the undergraduate and graduate levels. Also, during this period, he found time for a great deal of executive and committee work in the University of Alberta, scientific associations, the Fisheries Research Board of Canada, the National Research Council of Canada, and Alberta government agencies. He organized and was Director of the Alberta Biological Station. However, it was through his research that he became known and highly regarded by a wide group of scientific workers in freshwater biology and fisheries.

The major project during the first ten years of Dr. Miller's period at the University of Alberta was on *Triaenophorus*, a tapeworm of wide occurrence and considerable economic importance in freshwater fish. He made important contributions to our knowledge of the life history and ecology of this parasite, and carried out interesting experiments aimed at its possible control. Through his close cooperation with fisheries administrators in Alberta he developed an interest in the problems of fish populations and their exploitation. The confidence of the administration in him as a scientist made possible several noteworthy experiments in management which tested the effectiveness of whitefish planting and the effects of different fishing intensities. He also made biometric and life history studies on several important species of freshwater fish.

In his later years much of Dr. Miller's research was related to the problems of trout culture in streams. He was especially adept at applying a rigorous scientific approach to the practical problems of fisheries management. When his field experiments showed that hatchery-reared trout were not competing effectively with wild stock, he pressed on to studies of trout behaviour, demonstrating their habit of maintaining a home territory. In his latest work, he carried this investigation into the field of physiology, studying lactic acid and glycogen in relation to fatigue and death of hatchery-reared fish.

Dr. Miller was a founding member of the Canadian Conservation Association and a member of the New York Academy of Science, the American Fisheries Society, The Wildlife Society, American Society of Limnology and Oceanography, The Society of Systematic Zoologists, the International Association of Limnology, and an associate of the Arctic Institute of North America. He was a member of the National Research Council of Canada from 1956 and of the Fisheries Research Board of Canada from 1957 until the time of his death. In 1957 he served as Vice-President of the Wildlife Society. He was elected to fellowship in the Royal Society of Canada in 1959.

The results of his work are recorded in more than forty papers in scientific journals and in a large number of valuable interpretive articles in fish and game magazines.—D. S. RAWSON AND F. E. J. FRY.

BOOK REVIEWS

Fishes of the Great Lakes Region. By Carl L. Hubbs and Karl F. Lagler. Cranbrook Institute of Science, Bloomfield Hills, Michigan, Bulletin No. 26. Revised edition, 1958. xi+213pp., end paper map, 251 figs., 44 colored pls., $5.00.

Since its inception in 1941, as *Guide to the Fishes of the Great Lakes and Tributary Waters,* and later development (1947) into *Fishes of the Great Lakes Region,* this well-known and widely-used book has continued to increase in content and stature. In its present revised form, keys and illustrations for the identification of fishes of the region, and excellent, concise notes on the natural history of each fish, continue to comprise the major objective and bulk of the publication. However, the enlargement of introductory subjects further enhances the value of the book to ichthyologists and serious lay students of fishes.

The first 27 pages are given over to discussions of the Great Lakes waters and ichthyofauna, the distribution and post-glacial dispersal of fishes (enlarged from the 1947 edition), and directions for field study, collecting, preservation, and identification of fishes. The methods and terms of anatomical measuring and counting for taxonomic purposes are described with clarity. A classification of families of Great Lakes fishes according to schemes of Jordan and of Berg has been added to the text; the table is essentially that from Lagler's *Freshwater Fishery Biology.* The colored plates which in the 1947 edition were scattered throughout the book now number 44 and are grouped. Bibliographic references have been increased from 167 in the 1947 edition to nearly 250 in the revised version and include many recent works. The shape of the book has been changed and the quality of the paper improved.

Considerable modification, rearrangement, and enlargement is seen in studying the keys and illustrations relative to identifying fishes. The authors have seen fit to continue use of subspecific designations and have added 11 forms over the earlier edition. A chart for distinguishing the ciscos is a useful addition to the revised addition, and Figure 24, which in the 1947 edition left the uninitiated reader desiring illustration of both *Pomolobus pseudo-harengus* and *Alosa sapidissima,* now includes both. This latter point is mentioned specifically because a major fault of many taxonomists is that of using relative terms and then portraying only one of several possibilities; let us move away from the "darker than," "deeper than," "pelage denser than" school. A number of name changes have been recognized and incorporated by Hubbs and Lagler in their revision (*e.g., Cristivomer* to *Salvelinus, Leucichthys* to *Coregonus, Ameiurus* to *Ictalurus*). Rearrangement and changes in couplets of the dichotomous key are extensive [cf. *Catostomidae,* 1947 (p. 45) and 1958 (p. 58)]. Revisions have been made also in the section devoted to halftone illustrations. New illustrations have been substituted in some cases, and the figures of *Ictiobus niger* and *I. bubalus* have been transposed in the revision and fit the key descriptions better. It is unfortunate that some forms, particularly the madtoms, must be represented by most unlifelike examples.

In view of the failure of cost curves to reach an asymptote, it occurs to this reviewer to question the value of the colored plates, with respect to utility as well as to cost. Most of the forms in color are also reproduced in halftone and described in the key. Thus the inclusion of color seems to be based in esthetics.

It is truistic to say that this book is an indispensable tool of students of fishes of the Great Lakes region. Beyond its regional value the book indeed continues to be a major contribution to ichthyology generally.—GEORGE K. REID, Department of Zoology, Rutgers, the State University, New Brunswick, New Jersey.

A Field Guide to Trees and Shrubs. By George A. Petrides. Houghton Mifflin Company, Boston. 1958. xxix+431pp. $3.95.

A Field Guide to Trees and Shrubs is another one of The Peterson Field Guide Series, the first being Roger Tory Peterson's *A Field Guide to the Birds,* published in 1934. In this volume, the basic principle used in the series has been continued, namely, emphasis on visual differences and similarities rather than on taxonomic relationships.

The Guide is limited to woody plants that grow wild in northeastern and north-central United States and in southeastern and south-central Canada. It covers an area roughly bounded by a line from southern Virginia west to the 96th meridian, then north to the 49th parallel in Canada. In all, 645 species (186 genera) of trees, shrubs, and woody vines are discussed. Scientific names follow the eighth edition of Gray's Manual of Botany, as revised by Fernald. This was the primary guide for common names, although the U.S. Forest Service *Checklist of Native and Naturalized Trees of the United States* was also used as a guide for tree names. In a few instances, new common names are assigned.

Easily seen characteristics are emphasized and, as might be expected, particular attention is given to leaves, twigs, and buds. For selected species, 68 plates of diagrammatic drawings bring out key characters. A commendable feature is the short, mostly nontechnical descriptions of these characters placed beside the illustrations. The leaf and

bud drawings are by Petrides, and the flowers, fruit, and 12 pages of tree silhouettes are by Peterson. Leaves are shown in one tone of green.

The 13 pages on "How to Use This Book" cover a wide field of subjects from leaf types to climax vegetation. There are also subsections on species descriptions, the identification of unknown plants, and plant succession. These introductory statements are helpful to the beginner because they explain the plan of the book and provide a bit of information on plant ecology.

Through use of this book, the unskilled should be successful in identifying a woody plant that is in leaf. The scheme starts by placing the plant in one of five groups according to readily observed leaf characteristics; the next step is to key it out by such differences as growth habit, size, leaf form, and bud scales.

The species descriptions are, in most instances, sufficiently detailed to enable recognition of the plant one is trying to identify; in fact, the author uses a standard writeup under subheads of "recognition," "similar species," and "remarks." The latter often contain interesting information on use of the plant by man and/or wildlife. The illustrations are grouped and separate from the descriptions. Although this requires using two parts of the book simultaneously, it has the advantage of affording a quick check on leaf and bud drawings for a large group of similar plants.

The amateur botanist will be encouraged to learn more about the subject of classification. The appendix has keys based on winter conditions, and sections on "Plant Relationships" and "The Meaning of Botanical Terms."

George A. Petrides has been engaged in teaching and research in the field of natural science with the National Park Service and the Fish and Wildlife Service, and is now with Michigan State University. He has also found time for an extended period of study in the African big game country. His concept of the Guide took form when he was concerned with field-naturalist work in the National Park Service.

The task he undertook was not an easy one, since it involved simplifying taxonomic information and adapting it to a system of keys and descriptions based primarily on leaf, twig, and bud characteristics. In this process, plants unrelated botanically have sometimes been associated because they look similar. The descriptions will not satisfy persons who want precise information on flowers, fruits, and foliage. Any user, regardless of his training, will find the bud and twig drawings too small and simplified to use with confidence. Although taxonomic skills will help, it may be that the beginner with no training in the use of botanical keys has an advantage too—at least, such a person will not be bothered by the grouping of similar but unrelated plants.

Petrides has created an attractive and useful book. In fact, by substituting common descriptive words for technical terms, he has lost little in accuracy and the user has gained much in comprehension. *A Field Guide to Trees and Shrubs* should lead many more people to derive new pleasure from the outdoors through a better knowledge of woody plants.—LLOYD W. SWIFT, Forest Service, USDA, Washington, D.C.

American Agriculture: Geography, Resources, Conservation. By Edward Higbee. John Wiley & Sons, Inc., New York. 1958. x+399pp. $7.95.

Agriculture in the United States is an exceptionally diverse industry, currently in a state of rapid change. Because of the great variety of agricultural methods and commodities, it is extremely difficult for the nonspecialist to gain a clear understanding of agriculture over the entire nation. Edward Higbee's book presents a concise and factual account of this complex industry, and, as such, can be highly recommended as an introduction to an understanding of American agriculture.

American Agriculture should be of particular interest to workers in the field of wildlife management for several reasons. First, since a large portion of wildlife resources are associated directly with the farming enterprise, an understanding of agricultural production should aid the wildlife manager in appreciating the position of wildlife within the agricultural community. Second, since the harvest of wildlife resources will probably become more formalized as hunting pressures increase, wildlife managers will probably utilize some of the techniques of the agriculturalist to increase production of wildlife. For instance, the techniques of selective breeding, rearing, and feeding game species may be expected to become increasingly important. A knowledge of the geography and ecology of crop and animal production would allow the wildlife manager to better cope with the increasing pressures upon the wildlife resource.

Dr. Higbee's book is divided into two main sections, one dealing with the dry west and the other with the humid east. Western agriculture suffers from a lack of water, and in this connection, irrigation projects, the growth and decline of oases, and the value of forests in watershed protection are discussed. In the section on western agriculture the ranching areas, the dry plains, the Palouse, and the Willamette Valley are also considered in separate chapters. In contrast to the west, water is seldom a limiting factor in the eastern part of the United States, although drought does occur and irrigation can be practiced with success in many areas. Here topography plays a greater role in determining the intensity of land use. This is particularly evident in the Ozark–Appalachian region, where intensive agriculture should be practiced only in the river valleys or limestone lowlands, reserving the uplands for forestry or grazing. In the section on eastern agriculture the corn belt, cotton belt, dairying re-

gions, general farming areas, and specialty crop areas are considered in detail.

Throughout the book, the author uses one or more individual farms as examples of the type of farm organization in each agricultural area under discussion. Dr. Higbee has personally visited each farm mentioned in the text and has "walked across their fields and observed the good management of their operators." This method of citing specific illustrations results in a factual and interesting presentation. Without this approach, a survey book such as this could be lost in generalities. My own agricultural experience, based on actual farming and observation, is limited to only a few of the many regions mentioned; for these, the author's discussions are unusually clear in citing the problems and changing patterns of the local agricultural industry. In only one minor point would I wish to raise issue with the author; in his discussion of the increasing importance of forestry in the Southeast, he states that deliberate burning of forest undergrowth is a bad practice and is on the decline. This statement ignores the important work of Herbert Stoddard, who has shown that on the Georgia coastal plain controlled burning may be the best management for longleaf pine, and, in addition, provides excellent conditions for quail.

American Agriculture can be highly recommended to anyone wishing something more than the usual dry, fact-crammed, geographical–economic survey. Dr. Higbee's use of historical, geographical, and climatological data to provide an understanding of how agricultural patterns have developed results in a readable survey of agriculture in the mid-twentieth century in the United States.—FRANK B. GOLLEY, Dept. of Zoology, University of Georgia, Athens, Georgia.

The Ghost of North America. The Story of the Eastern Panther. By Bruce S. Wright. Vantage Press, Washington, D.C. 1959. xi+140pp., illus. $3.50.

This book contains chapters about the first appearance of the cougar in North America during prehistoric times, the period of ruthless destruction of the eastern panther after the first white settlement, the refugia of the few remaining panthers, and the recovery of the eastern subspecies within recent years. The author discusses in detail 28 observations from among over a hundred reported cases in the Northeast. He dedicates three chapters to various methods of studying the species. He also presents evidence on the movements of a yearling panther in New Brunswick, sightings of specimens in various parts of the East, and the panther's role in the East.

Wright makes an effort to combine factual information with popularized accounts, with the intention of appealing to as large an audience as possible. Although laudable, this effort does not turn out to be entirely successful from the biologists' point of view, because here and there he resorts to naturalists' jargon (see p. 90) without adequate reason. Although no specimens have become available during recent decades, the evidence presented leaves no room for doubt that the species is now living in parts of the Maritime Provinces and northern New England, and that there is a good possibility of its presence in other parts of the Northeast and Midwest. The author suggests that the eastern panther was saved from extinction because of an upsurge in the deer population and a change in habits. He pleads that it should be given recognition as a game animal. In his chapter on the art of reading sign, he provides details which are not generally known. It is unfortunate that the subspecific status of the southeastern form is not discussed on p. 14, where reference is made to other subspecies. No doubt *Felis concolor coryi* Bangs integrated with *Felis concolor couguar* Kerr. Similarly, the range of the southeastern form might have been indicated to good advantage on the map showing the range of the eastern panther. The other illustrations are generally satisfactory.

Wright's main contribution is to focus attention on the fact that the eastern panther, long thought to be extinct, is still with us and that, provided it is given adequate protection, it may remain an interesting component of our Eastern fauna.—ANTOON DE VOS, Ontario Agricultural College, Guelph, Ontario.

Animal Camouflage. By Adolph Portmann. University of Michigan Press, Ann Arbor. 1959. 111pp., 101 figs. $4.50.

The role of color, pattern, and form, in respect to artificial concealment or to resemblance to other objects, living or not, in the animal's environment, is of great interest to the biologist. Much controversy has raged as to how such results have come about through the evolutionary process. To the nature lover, who has the opportunity to observe these concealing or warning phenomena among the animals which share the world in which he lives and makes his playground, the results of the evolutionary process are a source of interest and wonderment. It is reasonable, therefore, that an exposition of the ways and means of camouflage in nature should have an appeal to both the professional biologist and the amateur.

Professor Portmann's book, originally written and published in German, has been translated into English for this edition by A. J. Pomerans. Its appeal should be broad. It is well written, in a lucid style, without unnecessary technicalities; it can be readily understood by the intelligent layman who has had no special training in zoology, but at the same time it carries a message for the profes-

sional. The illustrations are clear and well chosen, even though none are in color; some color would have helped, but lack of it does not hinder delivery of the message they are intended to convey. The illustrations are well distributed and remarkably well integrated with the text, so that the reader has the impression that he is following a series of illustrated lectures. On the other hand, the text is important; it is far more than a mere explanation of the figures.

The first chapter, "Camouflage and Vision," states the problem: the appearance of an animal is related to its survival; survival may depend upon either concealment from the seeing eye of an enemy, or upon flashing a warning to the enemy to beware: the brightly colored organism might be dangerous or distasteful. The second chapter, "Shape and Camouflage," discusses ways in which markings may blend with the landscape (including such phenomena as the "joining effect," in which the patterns of the fore and hind wing of a butterfly or moth may, together but not singly, produce an effective concealing design); it also takes up ways in which contours may be concealed, the animal may be masked by foreign objects, or the animal may be camouflaged through protective resemblance or mimicry. Some classical examples, such as the *Kallima* or dead-leaf butterfly, are used, but there are many unfamiliar and interesting illustrations of these principles.

The third chapter discusses concealing colors: their chemical and physical nature; their relations with the environment; and particularly adaptive color changes and the mechanics behind such phenomena. The fourth chapter, "The Significance of Camouflage," discusses briefly the significance of protective coloration and warning coloring in the light of experimental evidence. The "Conclusion," added as an epilogue, is somewhat disappointing; it merely shows, specifically in the case of the orange-tip butterfly, how remarkably protective resemblance and camouflage have aided the insect in each stage of its varied life cycle. Factually, it is satisfying; but perhaps we were expecting something more profound.

One small error might be noted. In the legend to Fig. 87, p. 76, what is referred to as the insect's "metathorax" is actually the scutellum, a part of the mesothorax. The unusual beetle-like fly pictured in this illustration is, in the reviewer's experience, one of the most remarkable examples of mimicry. — MAURICE T. JAMES, Department of Zoology, Washington State University, Pullman, Washington.

Georgia Birds. By Thomas D. Burleigh. University of Oklahoma Press, Norman. 1958. xxix+746pp., 35 color plates, 13 photos, 10 tables, 14 maps. $12.50.

This book opens with a 20-page chapter by William W. Griffin on the history of ornithology in Georgia, followed by 51 pages on the physiographic and biogeographic regions of the state by Robert A. Norris. Most of the volume consists of a review of the species and subspecies known to occur in the state, including, for each, sections on general distribution, status in Georgia, and habits and recognition. Subspecies are treated separately, the scientific and common names being given for each. Common names conform to those of the fourth (1931) edition of the American Ornithologists' Union Checklist and supplements. There is a hypothetical list of 27 species and a bibliography of 27 pages. The bulk of this book did not allow the inclusion of keys or sections on identification. The author's intensive collecting and field work, extending over a period of 25 years, made him eminently qualified for the preparation of this interesting book. Beautiful color plates by George M. Sutton add much to the attractiveness of the volume.— GEORGE E. HUDSON, Dept. of Zoology, Washington State University, Pullman, Washington.

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